VOLUME 64
NUMBER 5 / NUMÉRO 5
MAY / MAI
2007

An NRC Research Press
JOURNAL
Une REVUE des
Presses scientifiques du CNRC

Canadian Journal of FISHERIES AND AQUATIC SCIENCES

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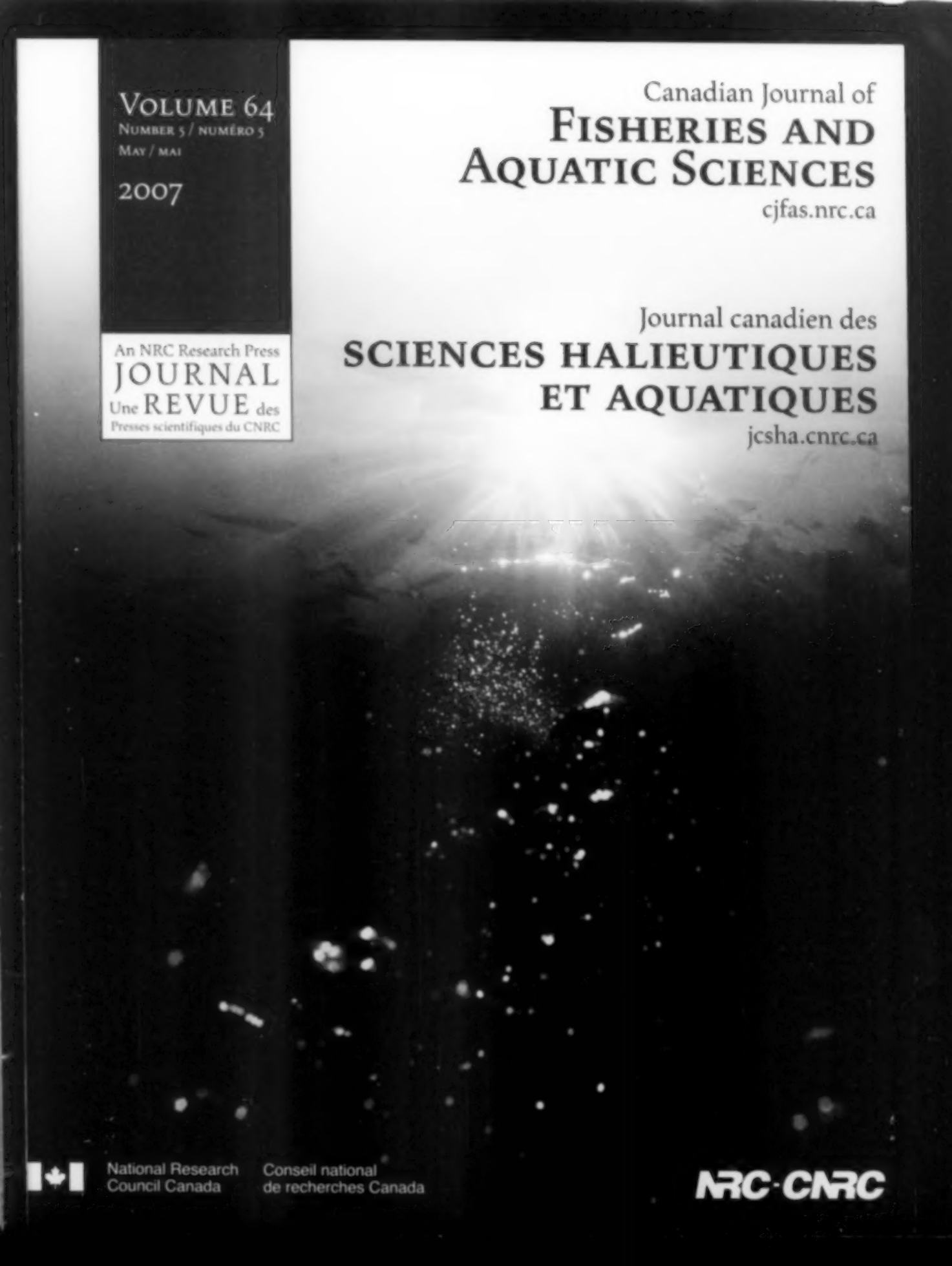

National Research Council Canada
Conseil national de recherches Canada

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ISSN 0706-652X / CJFSDX 64(5) 755–847 (2007)

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Volume 64, Number 5, May 2007

Canadian Journal of Fisheries and Aquatic Sciences

Published by the National Research Council of Canada

Volume 64, numéro 5, mai 2007

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Publié par le Conseil national de recherches du Canada

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Hydraulic geometry as a physical template for the River Continuum: application to optimal flows and longitudinal trends in salmonid habitat

Jordan S. Rosenfeld, John Post, Geneva Robins, and Todd Hatfield

Abstract: The River Continuum Concept lacks a quantitative physical model to represent downstream trends in habitat. We evaluate whether hydraulic geometry relationships can be used as a physical template to predict longitudinal trends in habitat availability and optimal flows for different life-history stages of rainbow trout (*Oncorhynchus mykiss*). Optimal flows based on hydraulic geometry indicate that (*i*) optimal flows are higher for larger fish, (*ii*) optimal flows proportionally increase as streams became smaller and decrease downstream, and (*iii*) maximum predicted habitat suitabilities for fry and juveniles are in small streams, and maximum suitabilities are displaced progressively downstream for later life-history stages. These patterns are an emergent property of downstream increases in channel depth and velocity and changes in habitat suitability curves associated with increased swimming performance of larger fish. Nonlinear downstream trends in habitat imply that fixed flow percentages recommended by the Tenant method may substantially underestimate optimal flows in small streams. Despite oversimplifying complex channel structure, hydraulic geometry relationships should serve as a useful physical model for testing downstream trends in habitat-related processes along the river continuum.

Résumé : Il manque au concept du continuum fluvial un modèle physique quantitatif qui puisse représenter les changements de l'habitat vers l'aval. Nous vérifions si les relations de la géométrie hydraulique peuvent servir de cadre pour prédire les tendances longitudinales dans la disponibilité de l'habitat et les écoulements optimaux pour les différents stades du cycle biologique de la truite arc-en-ciel (*Onchorhynchus mykiss*). La géométrie hydraulique indique que (*i*) les écoulements optimaux sont plus élevés pour les poissons de plus grande taille, (*ii*) les écoulements optimaux augmentent de façon inversement proportionnelle à la taille du cours d'eau et ils diminuent vers l'aval et (*iii*) la majorité des habitats optimaux prédits pour les alevins et les jeunes truites se trouvent dans les cours de plus petite taille; ces optimums se déplacent progressivement vers l'aval pour les stades plus avancés du cycle biologique. Ces patrons sont des caractéristiques qui résultent des augmentations vers l'aval de la profondeur du chenal et de la vitesse du courant, ainsi que des changements dans les courbes de qualité de l'habitat associées à l'augmentation de la performance de nage des poissons plus grands. Les tendances non linéaires vers l'aval dans l'habitat ont comme conséquence que les pourcentages fixes de débit recommandés dans la méthode de Tenant peuvent sous-estimer considérablement les débits optimaux dans les petits cours d'eau. Même si elles simplifient trop la structure complexe des chenaux, les relations tirées de la géométrie hydraulique devraient pouvoir servir de modèle physique utile pour tester les tendances vers l'aval dans les processus reliés à l'habitat le long du continuum d'un cours d'eau.

[Traduit par la Rédaction]

Introduction

Aquatic ecologists have long recognized that stream habitats change in predictable ways as they flow downstream, leading to longitudinal changes in biological communities and processes (e.g., Lotrich 1973; Naiman et al. 1987). The River Continuum Concept (Vannote et al. 1980) formalized the hypothesis that systematic habitat changes along a downstream gradient have predictable consequences for biological processes ranging from energy flow to community structure. Despite a general appreciation of the pervasive influence of physical habitat on biological processes in streams (e.g., Statzner et al. 1988; Rabeni and Jacobson 1993) and the dominance of the River Continuum Concept as the central paradigm in fluvial ecology, there has been surprisingly limited development and use of physical models to quantify downstream trends in habitat.

Systematic downstream changes in habitat are of particular interest to fish ecologists because they affect both the nature and quantity of habitat available for fish, and therefore

Received 30 May 2006. Accepted 25 November 2006. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 5 June 2007.
J19343

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 doi:10.1139/F07-020 © 2007 NRC Canada

longitudinal trends in fish abundance and community structure (Schlosser 1982; Lamouroux 2007). In particular, downstream changes in channel size and water velocity will alter the quantity of habitat suitable for different species (or life-history stages) based on factors like swimming performance that affect ability to exploit different habitats. Available habitat is therefore sensitive to (*i*) channel dimensions and velocity as affected by location on the river continuum and (*ii*) the amount of water in the channel at any given time (discharge), which increases systematically downstream and also varies according to the natural flow regime (Poff et al. 1997) and anthropogenic demands (Poff et al. 2003).

Downstream changes in channel structure will therefore influence changes in habitat availability in unperturbed systems, as well as differential effects of water abstraction on available habitat along the river continuum, an increasing concern as human demand for water increasingly conflicts with the needs of natural ecosystems (Postel et al. 1996; Vörösmarty et al. 2000). Fish biologists typically assess habitat availability in streams using the instream flow incremental methodology (IFIM) in conjunction with some form of physical habitat simulation model (e.g., PHABSIM) that describes how the distribution of depth, velocity, and substrate in a stream changes at different flows. A habitat suitability model for the species of interest is then superimposed on simulations to evaluate which flows are optimal (i.e., generate the maximum amount of useable habitat). To understand how fish habitat and optimal flows for rainbow trout (*Oncorhynchus mykiss*), steelhead (anadromous *Oncorhynchus mykiss*), Chinook salmon (*Oncorhynchus tshawytscha*), and brown trout (*Salmo trutta*) vary as a function of stream characteristics, Hatfield and Bruce (2000) performed a meta-analysis on 127 PHABSIM studies from streams and rivers in western North American ranging in discharge from 0.1 to 400 $m^3 \cdot s^{-1}$, representing the core of the native distribution of all three taxa. The most compelling pattern from their analysis was that optimal flows to maximize useable habitat varied systematically with stream size and location on the river continuum, confirming earlier observations from less comprehensive studies (e.g., Smith and Sale 1993; Jowett 1997). More specifically, optimal flows (as a percentage of mean annual discharge (MAD)) were found to generally increase as streams become smaller and decrease downstream, a pattern that was consistent for all four salmonid taxa. If there is a biological basis to this pattern, it has far-reaching implications for the management of stream flows, since the most common approach for determining instream flows in small streams (e.g., Tennant method; Tharme 2003) uses a fixed proportion of MAD irrespective of stream size.

As suggested by earlier studies (e.g., Jowett 1997), we hypothesize that downstream trends in habitat availability and optimal flows are the predictable outcome of interactions between downstream changes in average channel depth and velocity and the swimming performance characteristics of fish that influence habitat suitability. If this is the case, then the general patterns in both habitat availability and optimal flows observed by Hatfield and Bruce (2000) should be predictable using a physical habitat model that adequately represents the longitudinal habitat template in streams (e.g., downstream changes in depth and velocity; see Lamouroux and Capra (2002) for a similar analysis of the Hatfield and Bruce (2000) data set for brown trout).

In this paper, we explore the use of simple longitudinal hydraulic geometry relationships as a physical model to represent downstream trends in stream habitat. These relationships predict average channel width, depth, and velocity as power functions of stream discharge (eqs. 1, 2, and 3 below) and are a cornerstone of fluvial geomorphology (Leopold et al. 1964). Recent studies have demonstrated that average reach characteristics can be well-represented using simple hydraulic geometry relationships (e.g., Jowett 1998; Lamouroux and Jowett 2005). However, the suitability of simple hydraulic geometry relationships for representing longitudinal trends in fish habitat must be tempered by the observation that they implicitly ignore habitat complexity at smaller scales, effectively treating stream channels as uniform half-pipes, a gross oversimplification of channel complexity. Average estimates of channel depth and velocity from hydraulic geometry relationships fail to characterize (*i*) the small-scale heterogeneity associated with different substrate types and flows that create a patch mosaic in streams (e.g., Pringle et al. 1988), (*ii*) the transverse heterogeneity associated with shallow, slow water at stream margins and deep, fast water at the stream thalweg (Stewardson and McMahon 2002; Schweizer et al. 2007), (*iii*) or small-scale longitudinal variation in bed elevation associated with different habitat types (e.g., deep pools and shallow riffles). This small-scale complexity is pivotal to ecological processes in streams, and it is by no means certain that characterizing channels in terms of average characteristics — a single estimate of depth, velocity, and width at a section — can generate useful predictions of fish habitat and how it changes downstream.

Below, we describe the application of hydraulic geometry relationships to evaluating changes in fish habitat along the river continuum. We use both longitudinal (downstream) and at-a-station hydraulic geometry as a physical template to develop expectations for optimal flows and longitudinal trends in habitat availability for different life-history stages of rainbow trout (fry, juveniles, adults, and spawners) and compare our model predictions to empirical observations of optimal flows for rainbow trout from western North America (Hatfield and Bruce 2000). Our objectives are (*i*) to determine whether hydraulic geometry relationships can reproduce the empirically observed downstream trends in optimal flows for salmonids observed by Hatfield and Bruce (2000) (i.e., proportionally higher optimal flows in small streams; higher optimal flows for larger fish; and maximum habitat suitabilities for fry and juveniles in small streams); (*ii*) to provide a mechanistic basis for understanding why optimal flows may vary as a function of stream size; (*iii*) to determine how fish size or life-history stage affects expected longitudinal trends in available habitat; and finally, (*iv*) to evaluate the potential of hydraulic geometry relationships as a general physical template for predicting how biological processes change along the river continuum. We chose rainbow trout as the representative species for this analysis because it is widely distributed in streams and rivers, its biology (including habitat suitability curves) is well documented, and it showed qualitatively simi-

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lar downstream trends in optimal flows to the other salmonids (steelhead, Chinook salmon, and brown trout) studied by Hatfield and Bruce (2000).

Overview of longitudinal and at-a-station hydraulic geometry

Longitudinal hydraulic geometry

Leopold and Maddock (1953) were the first to formally describe downstream trends in average channel width, depth, and velocity as simple power functions of river discharge:

$$(1) \quad w = aQ^b$$

$$(2) \quad d = cQ^f$$

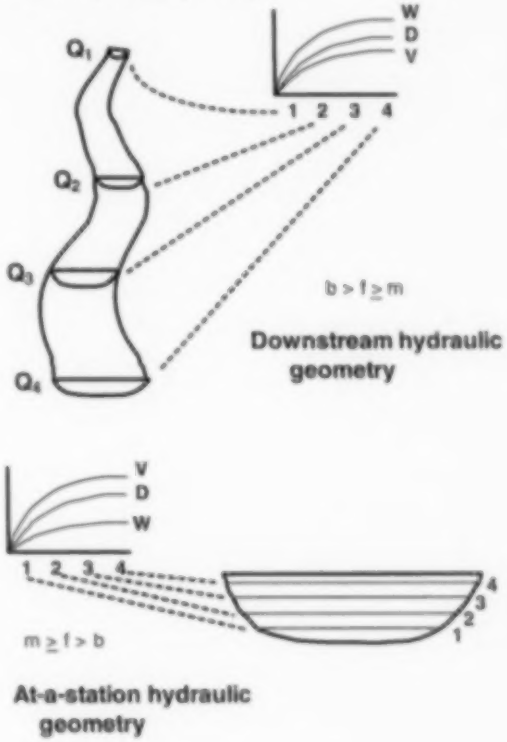
$$(3) \quad v = kQ^m$$

where w is average channel width; d is depth; v is velocity; Q is discharge; b, f, and m are exponents for the downstream rates of increase in width, depth, and velocity, respectively, with discharge; and a, c, and k are coefficients for the respective power functions. The assumption of continuity of discharge requires that the sum of the exponents equals 1 (i.e., an increase in depth requires a decrease in either width or velocity to maintain the same discharge), and similarly the product of the coefficients also has to equal unity ($b + f + m = 1$; $ack = 1$). These longitudinal relationships are empirically determined for a river basin by measuring channel width, depth, and velocity at multiple sites along a downstream gradient of increasing stream size at stable river flow (typically either bankfull stage or MAD, equivalent to average daily discharge; Fig. 1). The power function exponent is the slope of the log–log relationship, and the coefficient is the intercept; the coefficient can also be understood as the value of width, depth, or velocity when discharge is equal to 1 $m^3 \cdot s^{-1}$.

Because the exponents of the power functions are less than 1, the rates of increase of width, depth, and velocity decline as streams increase in size (Fig. 2). Differences in the rates of change of the three variables results in changes in average channel shape (e.g., width:depth ratio) along a downstream continuum. Because width invariably increases more quickly downstream than depth (modal values of b = 0.4–0.5; f = 0.3–0.4; m = 0.1–0.2; Park 1977), stream channels generally become relatively wider and shallower downstream, even though absolute width and depth increase with discharge. In essence, hydraulic geometry exponents describe the allometry of channel shape as streams increase in discharge.

The values of exponents range widely depending on the characteristics of a drainage basin (Park 1977; Richards 1977; Ferguson 1986), and differences in exponents represent an appealing way to characterize different types of streams with a minimum number of parameters, since exponent values change in predictable ways depending on basin gradient, substrate size, and riparian vegetation, among other factors (Hey and Thorne 1986; Millar 2005; but see Ridenour (2001) for a less optimistic view on consistent relationships between longitudinal hydraulic geometry and basin characteristics). Watershed gradient would appear to be the single most important factor influencing other exponents, with

Fig. 1. Downstream and at-a-station hydraulic geometry relationships. 1–4 represent either increasing discharge along a downstream continuum (upper panel) or increasing discharge at a single site (lower panel). The symbols b, f, and m represent the exponents for downstream rate of increase in width (W), depth (D), and velocity (V), respectively.



downstream velocity increasing more quickly (higher velocity exponent m) and depth more slowly (lower f) in steep basins (Fig. 2; Leopold et al. 1964), presumably as a consequence of greater roughness associated with larger substrate in steeper watersheds. The relationship between local slope and discharge can also be expressed as a power function, where

$$(4) \quad s = jQ^z$$

Unlike the exponents for other hydraulic geometry relationships, z is negative (i.e., local slope decreases with increasing stream discharge), and z is correlated with overall basin gradient. From this perspective, basin relief (steepness) can be viewed as an imposed constraint (Ferguson 1986) to which other factors (channel width, depth, and velocity) must adjust, although it should be recognized that fluvial geomorphologists also view local stream gradient as a response variable that adjusts to changes in sediment load and channel dimensions (Schumm and Lichty 1965). Average substrate size (roughness) appears to be the next most important factor influencing exponent values; an increase in average substrate size increases z (river gradient declines more slowly), thereby increasing downstream velocities (higher m; Leopold et al. 1964).

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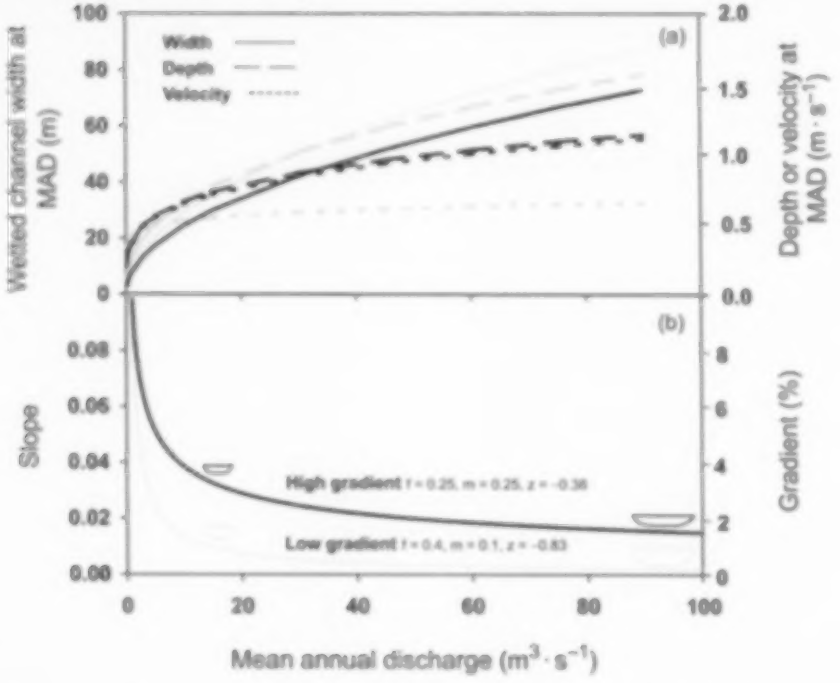
Fig. 2. (*a*) Downstream hydraulic geometry relationships for high-gradient (black lines) or low-gradient (grey lines) drainage basins. (*b*) Changes in slope along a downstream gradient of increasing discharge assuming an exponent for downstream rate of decrease in channel roughness of –0.2. MAD, mean annual discharge.



At-a-station hydraulic geometry

At-a-station hydraulic geometry describes the rate of change of channel width, depth, and velocity at a single site over a range of increasing discharge (Fig. 1) rather than at multiple sites at a single stage along the length of a river. The same power functions can be used to model at-a-station hydraulic geometry, but exponent values differ from downstream relationships. In contrast with downstream hydraulic geometry, width generally increases more slowly than either depth or velocity with increasing flow at a station (e.g., during a flood; Table 1). At-a-station hydraulic geometry parameters also vary with basin gradient (or watershed area; Dodov and Foufoula-Georgiou 2004), such that at-a-station velocity increases more quickly than depth in high-gradient basins (Table 1). Greater channel roughness associated with increased substrate size or bedform complexity also decreases the rate of change of velocity (*m*) and increases the rate of change in depth (*f*; Leopold et al. 1964; Hey and Thorne 1986; Knighton 1998). At-a-station hydraulic geometry has also been applied to describe changes in fish habitat with varying discharge at a single station (e.g., Hogan and Church 1989; Jowett 1998).

Materials and methods

Hydraulic modeling scenarios

To develop a physical habitat template for the river continuum, we used longitudinal hydraulic geometry relationships (eqs. 1–3; Fig. 1; Table 1) to describe how average channel width, depth, and velocity change with increasing discharge along a downstream continuum. (Discharge is viewed as a surrogate of distance from headwaters, since discharge is proportional to drainage area and therefore channel length (Knighton 1998). The absolute increase in channel length per unit discharge will depend on precipitation per unit area (i.e., streams in wet regions will generate greater discharge per unit area and therefore will have shorter channels for a given discharge).) Because basin gradient appears to be the single most important factor influencing longitudinal trends in channel morphology, we chose two contrasting sets of hydraulic geometry exponents representing high- and low-gradient basins to test how basin gradient affects downstream trends in fish habitat. Since velocity in high-gradient basins increases more quickly downstream (Fig. 2) to approach velocities that may exceed the tolerances of all life-history stages of fish (Fig. 3), we would predict that lower-gradient streams should have greater habitat availability at a given discharge, and therefore higher optimal flows for maximizing fish habitat. Note that a key assumption of our comparison of high and low gradient scenarios is a consistent relationship between longitudinal hydraulic geometry exponents and basin characteristics. Although supported by theory (Leopold et al. 1964), empirical support for this assumption is more ambiguous (e.g., Ridenour 2001; Wohl 2004).

For the high-gradient scenario, we used downstream and at-a-station hydraulic geometry exponents from a set of 73 New Zealand river reaches presented by Jowett (1998), with mean discharges ranging from 0.6 to 204 $m^3 \cdot s^{-1}$. Both downstream and at-a-station velocity coefficients for these

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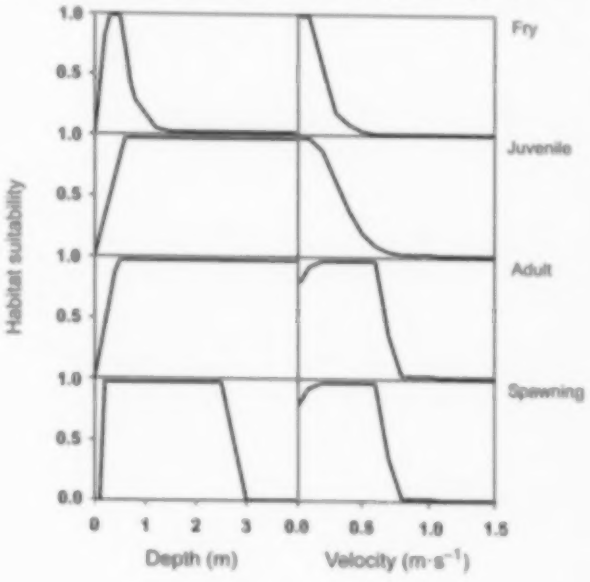
Table 1. Hydraulic geometry exponents and coefficients used in modeling scenarios.

	Downstream hydraulic geometry				At-a-station hydraulic geometry			
	Exponent		Coefficient		Exponent			
Parameter					Average		Riffle	
High gradient								
Width	b	0.5	a	7.8	b	0.21	—	—
Depth	f	0.25	c	0.37	f	0.34	f	0.44
Velocity	m	0.25	k	0.36	m	0.45	m	0.33
Low gradient								
Width	b	0.5	a	9.23	b	0.26	—	—
Depth	f	0.4	c	0.26	f	0.4	f	0.52
Velocity	m	0.1	k	0.42	m	0.34	m	0.22

streams tend to be higher (Table 1) than the averages presented by earlier reviews (Leopold and Maddock 1953; Park 1977), presumably reflecting the relatively steeper relief of New Zealand drainages (e.g., Biggs et al. 1990; Molnar and Ramirez 2002). For the low-gradient scenario, we used downstream and at-a-station exponents from the classic study of Leopold and Maddock (1953). Half of the rivers in the Leopold and Maddock (1953) data set came from low-relief topography in the central US plains (Kansas, South Dakota, and Nebraska), and the rest were from low- to intermediate-gradient rivers of the high western plateau (Wyoming, New Mexico, and Utah). Because the salmonid streams analyzed by Hatfield and Bruce (2000) came from the relatively steep topography of western North America (British Columbia, Alaska, Washington, Oregon, and California), we used the New Zealand (high gradient) exponents as the downstream model for comparing hydraulic geometry habitat predictions with empirical observations of optimal flows. (We implicitly assume that the higher longitudinal velocity exponent for New Zealand streams relative to the Leopold and Maddock data set is due to higher basin relief in New Zealand rather than differences in channel roughness exponent). We estimated z (the downstream rate of change of slope) in the low- and high-gradient scenarios as –0.38 and –0.83, respectively, using relationships derived from fig. 7–27 in Leopold et al. (1964; based on the Manning equation (Richards 1982), with $z = -3.16f + 1.4y + 0.65$, where y is the exponent for the relationship between channel roughness and discharge, and the width exponent is constant at $b = 0.5$). Assuming an average downstream rate of change of roughness of –0.2 (Leopold 1994) and substituting the equation for z above into eq. 4, f is related to local slope s as $f = [(\{[\log(s) - \log(j)]/\log(Q)\} - 1.4y - 0.65)/3.16]$. We estimated downstream change in slope assuming $j = 0.1$ (slope of 0.1 at $Q = 1$ m^3·s^{-1}).

To test the prediction that basin gradient affects longitudinal trends in habitat availability and optimal flows, we compared predictions of optimal flows between high- and low-gradient scenarios. Our simulations (and downstream hydraulic geometry relationships in general) are somewhat unrealistic in that they assume continuous longitudinal trends in channel metrics and river gradient. Real rivers exhibit downstream discontinuities in slope and sediment inputs (Ward and Stanford 1983; Poole 2002; Wohl 2004). These could be treated as local discontinuities in downstream exponents, but for simplicity we only consider continuous scenarios.

Fig. 3. Depth and velocity habitat suitability curves for different life-history stages of rainbow trout (*Oncorhynchus mykiss*).



We used the separate high- and low-gradient downstream hydraulic geometry relationships to estimate average channel width, depth, and velocity at MAD for 12 downstream stations (0.1, 0.5, 1, 3, 10, 15, 30, 45, 60, 75, and 90 m^3·s^{-1}) along a longitudinal gradient of increasing river discharge. At each of these 12 stations, we then used the corresponding high- or low-gradient at-a-station hydraulic geometry relationships to model how average channel width, depth, and velocity changed with increasing discharge at each station. Hydraulic geometry coefficients at each station were fit based on at-a-station exponents for low- or high-gradient scenarios (Table 1) and the estimates of wetted width, depth, or velocity imposed by downstream hydraulic geometry. Fitted hydraulic geometry coefficients showed relationships with stream discharge similar to those observed elsewhere (e.g., Stewardson 2005). To provide a more intuitive metric of stream size for comparative purposes, we also estimated

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channel bankfull width as a function of discharge, assuming that MAD was on average 13% of bankfull discharge (Leopold 1994). (This assumption will tend to overestimate channel bankful width when MAD is a higher proportion of bankfull discharge.)

Estimation of optimal flows along a downstream gradient

We used rainbow trout habitat suitability curves (Raleigh et al. 1984; Fig. 3) to calculate habitat suitability and weighted useable area over a range of flows at each downstream station for each life-history stage of rainbow trout (fry, juveniles, adult, and spawning; Fig. 4). Habitat suitability curves are generally based on frequency of use of different microhabitats in the wild and are standardized to a maximum of 1 (Bovee 1982; Mathur et al. 1985). Estimates of optimal flow using IFIM and PHABSIM typically use habitat suitability curves for depth, velocity, and substrate; we used suitability curves for velocity and depth only, since hydraulic geometry models do not predict substrate size. IFIM generates estimates of weighted useable area (WUA, a composite of habitat quality and habitat area) by multiplying the habitat suitability values associated with modeled depth, velocity, and substrate in each PHABSIM habitat cell to derive a composite habitat suitability score, which is then multiplied by cell area to generate WUA per cell; cell values of WUA are then summed for a site (Bovee 1982; Parasiewicz and Dunbar 2001).

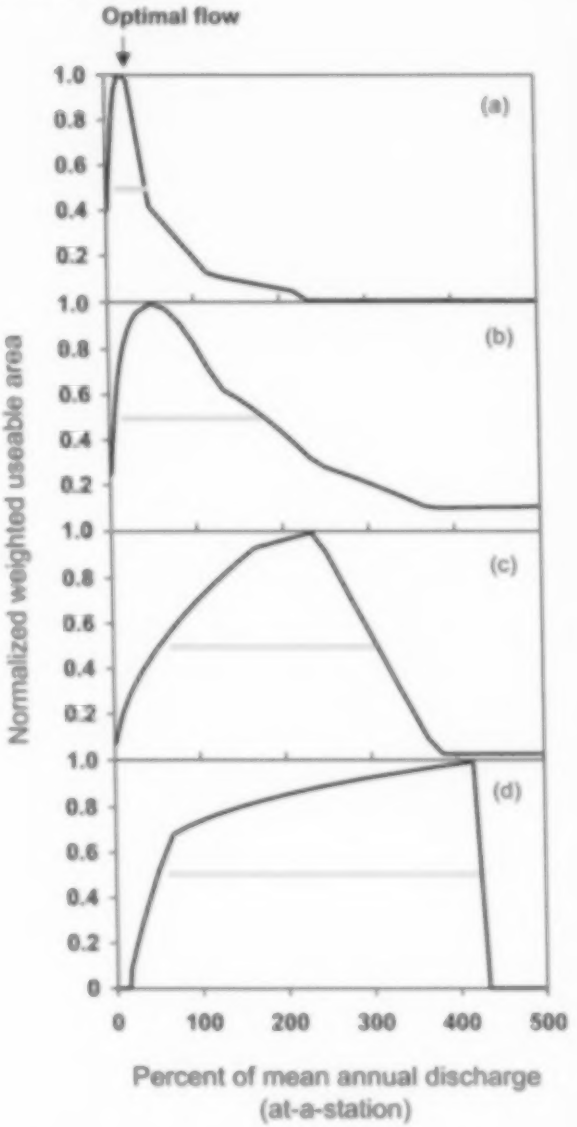
We converted mean velocity and depth estimated using hydraulic geometry to modal velocities and depths by multiplying by 0.87 and 0.79, respectively (after Jowett 1998), to generate modal estimates that more accurately represent available habitat for skewed distributions. To estimate WUA with our simplified hydraulic geometry data, we calculated WUA at multiple discharges at each station based on the product of the habitat suitability values for average channel depth and velocity multiplied by channel wetted width. Optimal flow was determined as the flow that maximized WUA for each life-history stage (Fig. 4). Habitat suitability curves and the WUA approach have a variety of shortcomings that compromise their ability to accurately represent true habitat quality (e.g., Mathur et al. 1985; Rosenfeld 2003; Rosenfeld et al. 2005); however, the estimates of useable habitat and optimal flows summarized by Hatfield and Bruce (2000) are based on IFIM and WUA, constraining us to use the same approach for comparative purposes. While estimates of WUA may provide poor estimates of habitat quality, they may provide a more reasonable representation of the amount of habitat that falls within the performance limits of a particular life-history stage (Rosenfeld et al. 2005).

Refinement of optimal flow predictions using pool–riffle hydraulic geometry

Because hydraulic geometry relationships estimate average channel characteristics and ignore variance in velocity and depth, they may provide poor estimates of habitat availability for organisms using habitats with higher or lower velocities than the channel average. For example, if spawning fish use high-velocity riffle habitat (Fig. 3), average channel velocities will underestimate the velocity of their preferred habitat at a given discharge and therefore overestimate optimal flows. To test whether incorporating heterogeneity in velocities and depths associated with pool and riffle structure could improve predictions of optimal spawning flows, we also estimated optimal spawning flows using different at-a-station hydraulic geometry parameters for pool and riffle habitats.

The effect of pool and riffle habitat on at-a-station rates of change in velocity and depth is well documented (Richards 1977; Knighton 1998) and has been described as velocity re-

Fig. 4. Weighted useable area vs. discharge at a single station (mean annual discharge (MAD) = 3 $m^3 \cdot s^{-1}$) for rainbow trout (*Oncorhynchus mykiss*) fry (*a*), juveniles (*b*), adults (*c*), and spawners (*d*). Weighted useable area is divided by the maximum at a site to standardize to a value of 1. Grey lines represent the range of discharge over which the weighted usable area exceeds 50% of the maximum.



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versal or flow convergence (Wilkinson et al. 2004). At bankfull stage, differences in bed elevation associated with pools and riffles exert less influence on total water depth, so that velocities and depths tend to converge across habitats. At low discharge, pools are deeper and slower than riffles, but as stream flow increases with a rising hydrograph velocity in pools increases more quickly than velocity in riffles (Fig. 5), leading to velocity reversal if pool velocity exceeds riffle velocity. In effect, pools may switch from being depositional habitats at low flows to erosional ones at high flows, with the opposite being true for riffles. Associated differences in the hydraulic geometry exponents for pools and riffles have been observed (Richards 1977; Knighton 1998). We modeled velocities and depths in riffle habitats by symmetrically increasing the depth exponent and decreasing the velocity exponent by 0.12 (Fig. 5; Table 1), a value that approximates the differences in exponents between pools and riffles observed in a number of studies (e.g., Richards 1977; Knighton 1998; Halket and Snelgrove 2005).

To derive coefficients for riffle hydraulic geometry equations, we estimated riffle depth by first modeling residual pool depth (RD_{pool}) as a function of bankfull channel width (W_{bf}; $R^2 = 0.67$, $F_{1,51} = 10.4$, $P < 0.024$) using data from rivers in California (Madej 1999; using the 75th percentile of pool depths from 1995 when channels were least aggraded):

$$(5) \qquad RD_{pool} = 0.057(W_{bf})^{0.534}$$

Total pool depth at a given discharge was estimated as the sum of average depth (predicted by hydraulic geometry) and residual pool depth, and average pool velocities were estimated based on continuity of discharge. Increased velocity in riffles was assumed symmetrical with decreased velocity in pools, and riffle depth was estimated assuming continuity of discharge. We assumed equivalent widths in pools and riffles.

Downstream trends in habitat suitability

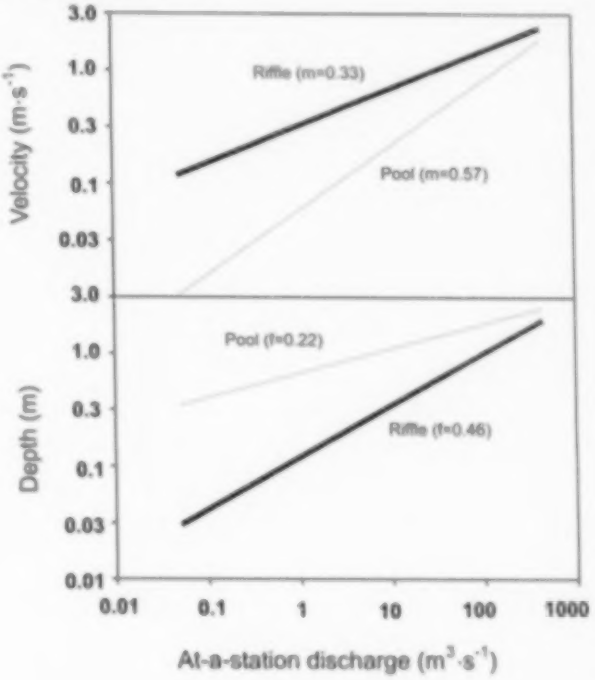
Longitudinal trends in fish abundance and habitat suitability represent the interaction of performance tolerances of different life-history stages (Fig. 3) and downstream increases in velocity and depth. For instance, if smaller fish have lower maximum sustained swimming speeds, then habitat suitability for fry and juveniles should decline as velocities increase downstream. To evaluate how habitat suitability for different life-history stages is expected to change along a downstream continuum, we modeled habitat suitability and WUA for fry, juveniles, adults, and spawners at all 12 downstream stations at MAD.

Results

Observed vs. modeled longitudinal trends in optimal flows

Hatfield and Bruce (2000) fit power functions to empirical estimates of optimal flows for different life-history stages (Fig. 6*a*), which clearly show that optimal flows (as a percentage of MAD) are (*i*) higher in smaller streams and (*ii*) progressively higher for larger life-history stages. Predicted optimal flow curves based on hydraulic geometry reproduced both of these attributes (Fig. 6*b*). Optimal flows for individual life-history stages predicted by hydraulic geometry (Fig. 6*b*) showed the same general shape as the empirical relationships from Hatfield and Bruce (2000), with predicted optimal flow as a proportion of MAD higher in small streams. Hydraulic model predictions also ranked optimal flows for different life-history stages in the same order, with highest optimal flows predicted for spawning habitat, followed by adult, juvenile, and fry habitat. The actual precision with which hydraulic geometry predicted the best-fit line to average optimal flows observed by Hatfield and Bruce (2000) was far less accurate and generally outside of the 95% confidence intervals of the empirical relationships (Fig. 7). Optimal flows for fry and juveniles were generally underestimated using hydraulic geometry (Fig. 6*b*), and optimal flows for adults and spawners were systematically overestimated.

Fig. 5. Contrasting rates of change of velocity and depth with increasing discharge in pools and riffles (for mean annual discharge (MAD) = 3 $m^3 \cdot s^{-1}$).



The overestimate in predicted optimal flows was most pronounced for spawning habitat (S_s, Fig. 6*b*; Fig. 7). Optimal flows estimated using habitat suitability and WUA in riffle habitat (i.e., using riffle hydraulic geometry exponents rather than channel average exponents) dramatically improved the shape and accuracy of the optimal flow curve for spawning (S_r, Fig. 6*b*). This supports the expectation that incorporating variance in velocity and depth associated with smaller-scale habitat structure (i.e., including the distribution of velocity and depths rather than average values) greatly improves predictions of habitat availability and optimal flows.

The implicit assumption of the Tennant approach that optimal flows are independent of stream size was not substanti-

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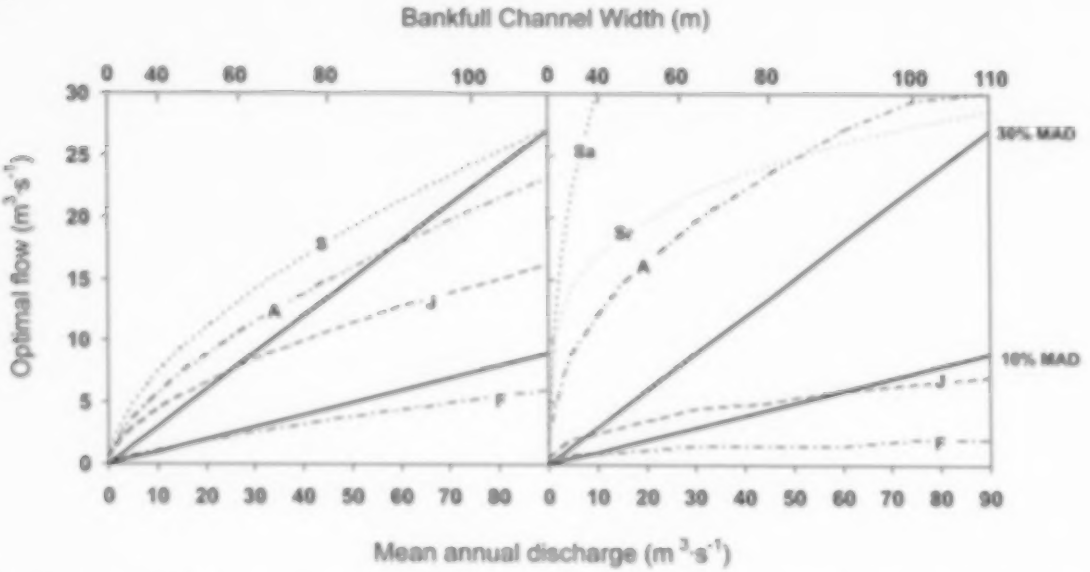
Fig. 6. Observed (*a*) and modeled (*b*) optimal flows for different life stages of rainbow trout (*Oncorhynchus mykiss*) plotted against mean annual discharge (MAD) along a downstream gradient. Modeled habitat availability and optimal flows use hydraulic geometry exponents for steeper drainages from Jowett (1998). F, fry; J, juveniles; A, adults; S, spawning; S_a and S_r represent spawning habitat modeled using average or riffle depth and velocities, respectively. Straight lines represent Tennant (1976) flow criteria of 10% and 30% of MAD.



ated by either the empirical or hydraulic model relationships. Deviation of predicted optimal flows from Tenant recommendations (i.e., straight lines representing 10% and 30% MAD in Fig. 6) is greatest for very small and very large streams. The Tennant instream flow recommendations (10% MAD as a minimum short-term flow for aquatic organism survival, 30% MAD as good conditions, and 60% MAD as optimal; Tennant 1976) fit reasonably well with the empirically observed optimal flows for fry in small streams with MAD < 1 $m^3 \cdot s^{-1}$ (Fig. 7), although they fall below the optimal flows for fry predicted by hydraulic geometry. However, optimal flows for juveniles predicted by both empirical and hydraulic geometry relationships greatly exceed the fixed Tennant recommendations in small streams (Fig. 7). Hydraulic geometry modeling also indicates that fry and juvenile habitat is most sensitive to deviation from optimum (narrow peaks in WUA; e.g., Fig. 4), likely as a consequence of the narrower depth and velocity tolerances of early life-history stages (Fig. 3).

Longitudinal trends in habitat in high- vs. low-gradient basins

As expected, optimal flows for the low-gradient scenario exceeded those of the high-gradient scenario for most life-history stages (Fig. 8). Higher optimal flows also imply greater available habitat at optimal flow in lower-gradient streams; for example, estimates of WUA were on average 1.5 times higher for fry and 4 times higher for juveniles in the low-gradient scenario. This modeling indicates that optimal flows are sensitive to basin gradient as well as stream size, causing fixed-flow Tennant recommendations to further underestimate optimal flows in low-gradient streams. Closer fit of modeled to empirical optimal flows using the New Zealand high-gradient hydraulic geometry exponents supports the assumption that they are more representative of the relatively steep topography of the data set analyzed by Hatfield and Bruce (2000) than exponents from the lower gradient rivers sampled by Leopold and Maddock (1953).

Downstream trends in habitat suitability by life-history stage

Longitudinal trends in habitat suitability and WUA at mean annual discharge in the high-gradient scenario indicate that habitat suitability for fry peaks in the smallest streams (<5 m bankfull channel width; Fig. 9) at MAD, habitat suitability for juveniles peaks at ~10 m bankfull channel width, and habitat for adults and spawners peaks at channel widths on the order of 40 m. WUA generally peaks further downstream than habitat suitability, indicating that declining habitat suitability downstream may be partially offset by increasing area of useable habitat as channels become wider. As discharge decreases, optimal habitat for all life stages tends to be displaced downstream (Fig. 9).

Predictions of habitat suitability and WUA for adults goes to zero downstream, highlighting the limitations of using average channel depth and velocity to calculate habitat suitability and WUA. When the average downstream channel velocity exceeds the threshold suitability limits of adult fish (Fig. 3), predicted WUA based on channel averages goes to zero; using a frequency distribution of depths and velocities (i.e., incorporating variance in velocity and depth associated with slower pools and channel margins; Lamouroux et al. 1995; Stewardson and McMahon 2002) would remedy this anomaly and more realistically predict the presence of suit-

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able habitat at higher average channel velocities. It is also worth noting that we have greater confidence in our estimates of optimal flows than WUAs, since the location of the peak in optimal flow (Fig. 4) will be insensitive to consistent biases in WUA estimates.

Discussion

Despite their simplicity, basic hydraulic geometry relationships reproduced the general longitudinal trends in optimal flows observed for salmonid streams in western North America. Hydraulic geometry relationships demonstrated that (*i*) optimal flows are higher for larger fish (later life-history stages), (*ii*) optimal flows (as a percentage of MAD) generally increase as streams became smaller and decrease downstream, and (*iii*) maximum predicted habitat suitabilities for fry and juveniles are in small streams, and maximum suitabilities are displaced progressively downstream for later life-history stages and lower flows. These are the same conclusions drawn by Hatfield and Bruce's (2000) empirical analyses of 127 PHABSIM studies for stream salmonids from western North America. These conclusions are also supported by an earlier reanalysis of the Hatfield and Bruce (2002) data set by Lamouroux and Capra (2002), who also demonstrated that optimal flows for adult brown trout could be predicted from simple reach characteristics (width, depth, discharge, and bed grain size).

The observed longitudinal trends in habitat and optimal flow are an emergent and predictable outcome of size-related performance tolerances of fish (as represented by habitat suitability curves) and downstream hydrology (increases in depth and velocity) along the river continuum. For example, the generally lower velocity and depth preferences of smaller fish tend to constrain their optimal habitat to smaller streams. While the shape, order, and magnitude of optimal flow relationships from hydraulic geometry were similar to observed relationships, model predictions were usually outside of empirical confidence intervals. In the form presented here, hydraulic geometry relationships should be viewed as a habitat template (process) model that captures general downstream trends and patterns rather than as a predictive model for estimating optimal flows for individual streams. Moving towards empirical models of longitudinal trends in habitat availability and optimal flows based on hydraulic geometry will require further empirical studies relating hydraulic geometry parameters to basin characteristics.

Nevertheless, the concordance of optimal flow predictions with empirical relationships is remarkable, given the simplifying assumptions involved. For instance, the published hydraulic geometry parameters that we applied to high-gradient streams came from a landscape (New Zealand) with similar relief to the reference data set (western North America), but we have no way of knowing how accurately they represent the true reference stream parameters. Similarly, the individual studies summarized by Hatfield and Bruce (2000) estimated optimal flows using a variety of different habitat suitability curves for rainbow trout, often based on observations of habitat use in individual streams. Many of these instream flow studies also used habitat suitability curves for substrate in their estimation of WUA, while our simplified estimates were based solely on velocity and depth. Given these multiple sources of error, the fit of the hydraulic geometry predictions is surprisingly good and indicates that the general form of the underlying relationships (and therefore the inferences that can be made from them) is extremely robust. This is supported by the observation that Hatfield and Bruce (2000) observed qualitatively similar relationships for both steelhead and Chinook salmon.

The main shortcoming of downstream hydraulic geometry for estimating fish habitat is that estimates of average channel velocity and depth, even when extremely accurate, lead to biases in habitat availability because the variance (i.e., the proportion of habitat above and below the mean) is undescribed (Singh and Broeren 1989; Moody and Troutman 2002). For example, at flows where mean velocities exceed the tolerance of fry (0.5 m·s^{-1}), predicted fry habitat based

Fig. 7. Observed and modeled optimal flows as a percentage of mean annual discharge (MAD) for (*a*) adult (A) and spawning (S) rainbow trout (*Oncorhynchus mykiss*) and (*b*) fry (F) and juveniles (J). Broken lines are observed optimal flows (F_O, J_O, A_O, S_O) from Hatfield and Bruce (2000), and solid lines are modeled optimal flows (F_M, J_M, A_M, S_M) using high-gradient hydraulic geometry exponents from Jowett (1998). Horizontal lines represent 10% and 30% of MAD. Broken grey lines represent 95% confidence intervals for estimates of observed optimal flow from Hatfield and Bruce (2000).

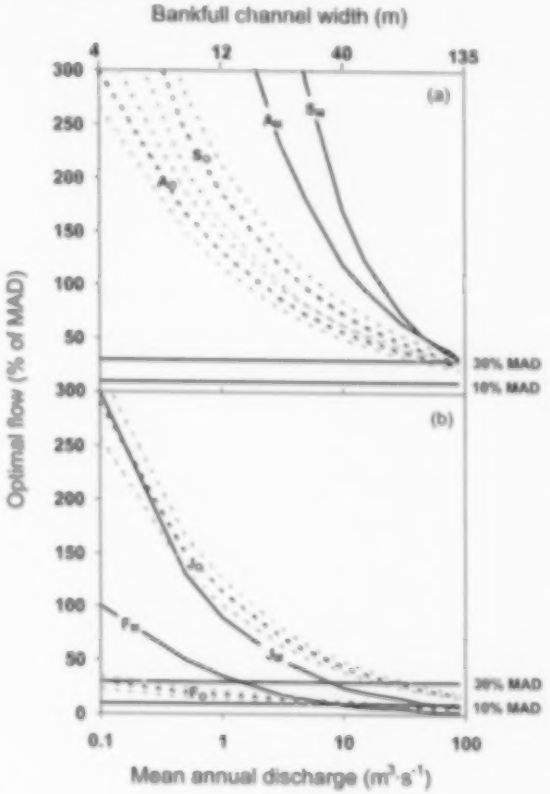

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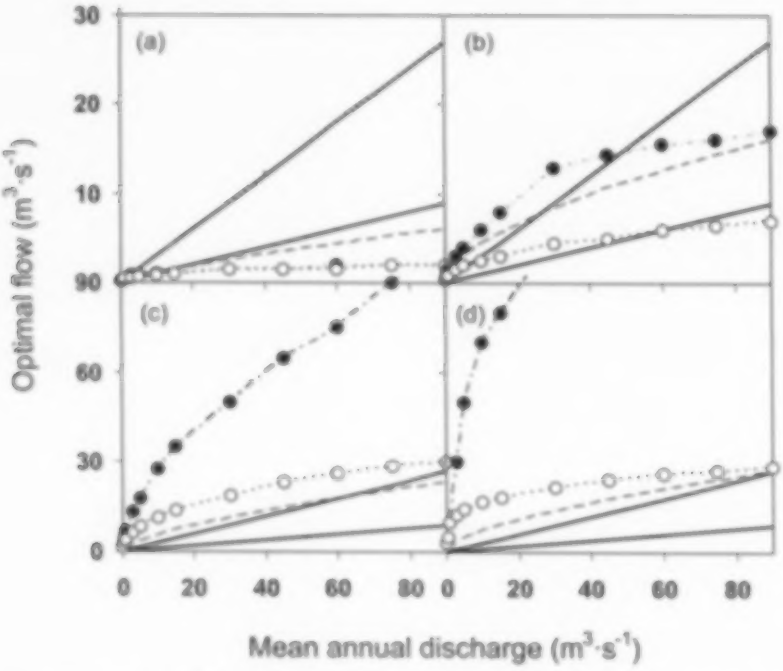
Fig. 8. Predicted optimal flows for high-gradient (open circles) and low-gradient streams (solid circles) by life-history stage: (*a*) fry, (*b*) juvenile, (*c*) adult, (*d*) spawners. The broken line without symbols represents observed optimal flows from Hatfield and Bruce (2000). Solid lines represent Tennant (1976) flow recommendations of 10% (lower line) and 30% (upper line) mean annual discharge (MAD).



on channel means will be zero, even though fry habitat may be present in shallow water at stream margins (Rao et al. 1993). The predictive value of accounting for small-scale heterogeneity in channel structure is demonstrated by the improved fit of optimal spawning flows when riffle hydraulic geometry exponents are used. This approach, however, still provides only a mean estimate of channel depth and velocity in riffle habitat. A frequency distribution of depths and velocities at a site, rather than a simple mean, should provide much more accurate estimates of useable habitat and optimal flows (Rao et al. 1993). Distributions can be generated directly from empirical measurements or from probabilistic models that predict the frequency distribution of depth and velocity around average values (e.g., Lamouroux et al. 1995; Stewardson and McMahon 2002; Schweizer et al. 2007). Recent models that predict the joint probability distribution of depth and velocity (e.g., Schweizer et al. 2007) may prove to be a more robust approach to account for longitudinal variation in velocity and depth than the use of different hydraulic geometry exponents for pools and riffles, as presented here.

The most directly applied result of our analysis is that optimal flows must vary as a function of stream size, as previously noted by Hatfield and Bruce (2000) and earlier authours (e.g., Annear and Conder 1984; Smith and Sale 1993; O'Shea 1995; Lamouroux and Capra 2002). The application of fixed-proportion-of-flow criteria (e.g., Tennant approach) irrespective of channel size may therefore seriously under- or over-estimate optimal flows depending on stream size. This is most pronounced for small streams and larger rivers, where the deviation from Tennant recommendations is greatest. Underestimation of optimal flows is of greatest concern for smaller streams, which are rarely allocated the resources for a formal flow assessment and therefore default to fixed-proportion-of-flow management. While the empirically estimated optimal flows for fry fall within the recommended Tennant flow range for channel widths <12 m, both empirical and modeled optimal flows for juveniles greatly exceed even the Tennant recommendation of excellent flows (60% MAD) at channel widths <20 m (3 $m^3 \cdot s^{-1}$ MAD). If the fish population of interest is limited by abundance of juveniles rather than fry (often the case for many salmonids, e.g., anadromous cutthroat trout (*Oncorhynchus clarkii*) or steelhead), then the Tennant flow recommendation may be inappropriate and have the potential to substantially impact a population. If the population is limited by adult habitat (e.g., resident fish), then even higher flows may be required.

Overestimation of optimal flows in larger rivers using the Tennant approach is probably less of a management concern than underestimation of flows in small streams. Modeled and observed optimal flows for adults are above or close to 30% MAD even for the larger stream size in our analysis (90 $m^3 \cdot s^{-1}$ MAD). Although lower flows are predicted to be optimal for fry and juveniles in larger streams, if juvenile life stages are not limiting the population because of abundant rearing habitat in smaller tributaries, then downstream flows should be managed to maximize habitat for adults (i.e., higher rather than lower flows).

This also highlights two potentially competing objectives of flow regulation: maximizing the amount of habitat for a

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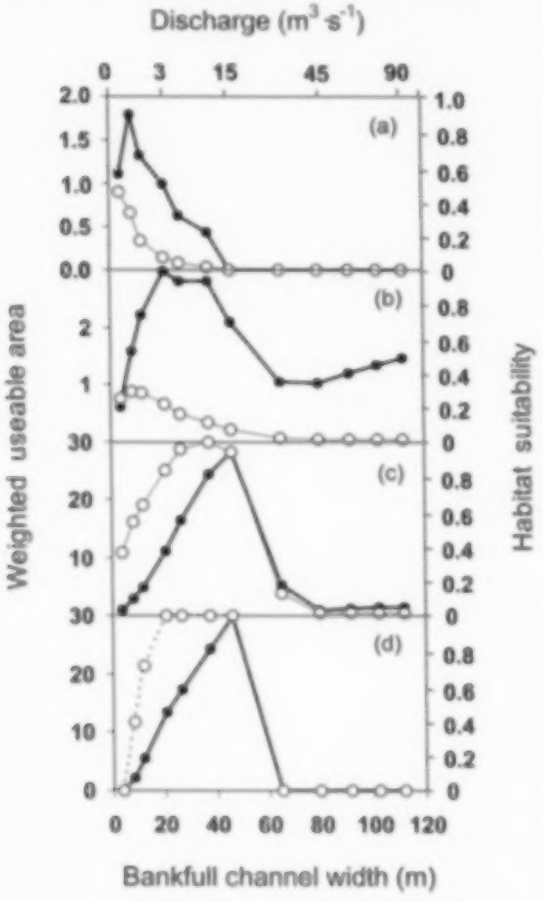
Fig. 9. Weighted useable area (solid circles) and average habitat suitability (open circles) vs. channel width or longitudinal discharge for fry (*a*), juvenile (*b*), adult (*c*), or spawning (*d*) rainbow trout (*Oncorhynchus mykiss*) at mean annual discharge.



target species or life-history stage vs. maintaining a natural flow regime that maximizes biological integrity of the natural system (Orth 1987; Jowett 1997; Poff et al. 1997). Managing flows for a single juvenile life stage requires maintaining higher flows in smaller streams and relatively lower flows in larger ones, leading to convergence of hydraulic conditions on an optimum defined by the habitat suitability curves of a taxon that tends to reduce the natural contrast in stream character along the river continuum (Jowett 1997). If the management goal throughout a river profile is to maximize abundance of juvenile salmonids with lower velocity requirements, then differentially reducing flows in larger downstream reaches may facilitate this goal. However, if the goal is to maintain suitable biological conditions for the suite of life-history stages, species, and processes that normally occur in longitudinal succession along the river continuum, then managing for low flows that create optimal habitat for a single juvenile life stage may be inappropriate (Tharme 2003; Anderson et al. 2006). Restoration of lower-velocity side-channel habitat along river main stems may be a more appropriate way to increase juvenile habitat without adversely affecting other species or biological processes that are dependent on higher flows. In contrast, managing for higher base flows in smaller streams may be appropriate when juvenile salmonids are the most abundant taxa present in a low-diversity system, as is often the case.

Our analysis also needs to be tempered by the understanding that the logic behind WUA as an index of habitat availability is flawed for a number or reasons (Mathur et al. 1985; Garshelis 2000). For instance, a large area of marginal habitat (e.g., velocity and depth suitability <0.25) can generate the same WUA value as a small area of highly suitable habitat, even though the marginal habitat may not permit substantial growth or survival. Even if WUA gives an accurate representation of available habitat, changes in flow simultaneously affect habitat for multiple life-history stages as well as the production of their prey, making it difficult to infer population-level effects based on changes in WUA alone. The WUA–IFIM approach cannot predict a population response without some understanding of the effect of habitat on abundance, population limitation, and recruitment of individuals between life stages (Kocik and Ferreri 1998; Gouraud et al. 2001; Railsback et al. 2003), that is, populations may be limited by habitat for fry, juveniles, or adults (Capra et al. 2003; Anderson et al. 2006; Rosenfeld and Hatfield 2006). To truly understand the population-level effects of changes in flows, flow models that predict changes in habitat need to be linked to stage-structured population models (e.g., Sabaton et al. 1997; Bartholow et al. 2001; Gouraud et al. 2001) within a landscape context (Fausch et al. 2002). Ideally, these models should also account for flow effects on processes other than fish habitat, such as effects of flow on production of invertebrate prey, maintaining temperature or water quality in a nonlethal range, or maintenance of channel structure, to name a few (White 1976; Jowett 1997; Anderson et al. 2006).

Our hydraulic geometry analysis also ignores transverse structure associated with the floodplain (e.g., side-channel habitat) and habitat that may become available at flood discharges (i.e., floodplain habitat); in tropical rivers, juvenile rearing habitat may be most abundant at extremely high flows rather than extremely low flows (Junk et al. 1989). Similarly, side-channel and floodplain habitat that is wetted at low to moderate flows in temperate rivers is not captured by simple hydraulic geometry, but is especially important because it displaces juvenile rearing habitat much further downstream than it would normally be predicted to occur when a channel is modeled as a half-pipe.

A hydraulic geometry approach to characterizing physical habitat can be potentially useful in both a landscape and River Continuum context. In a landscape context (Fausch et al. 2002), hydraulic geometry can be used to characterize habitat patches within a drainage network, where the distribution of habitat patches suitable for different life-history stages and the ability of fish to move between them ultimately determine the size and viability of populations (Schlosser 1991, 1995; Kocik and Ferreri 1998). In a River Continuum context, our analysis of optimal flows indicates that hydraulic geometry can be successfully applied as a habitat template to test explicit hypotheses of longitudinal change in ecological processes along the river continuum. While hydraulic geometry relationships performed reason-

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ably well for predicting optimal flows, the inclusion of small-scale habitat structure (e.g., longitudinal and transverse heterogeneity in channel depth and velocity; Stewardson and McMahon 2002) will generate much more realistic estimates of available habitat. Future model refinement should focus on (*i*) including depth and velocity distributions based on empirical data or probabilistic models (e.g., Schweizer et al. 2007) and (*ii*) estimating habitat availability at a drainage network scale by taking into account the abundance of streams of different sizes within a basin.

Acknowledgements

We thank Nicolas Lamouroux, Andrew Paul, and several anonymous reviewers for providing useful feedback on this manuscript. Financial and administrative support was provided by the Alberta Ingenuity Center for Water Research.

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Optimal growth temperature hypothesis: Why do anchovy flourish and sardine collapse or vice versa under the same ocean regime?

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Abstract: The out-of-phase population oscillations between anchovy and sardine have been attributed to climate changes. However, the biological processes causing these species alternations have remained unresolved. Here we propose a simple "optimal growth temperature" hypothesis, in which anchovy and sardine regime shifts are caused by differential optimal temperatures for growth rates during the early life stages. Dome-shaped relationships between growth rate and sea temperature were detected for both Japanese anchovy (*Engraulis japonicus*) and Japanese sardine (*Sardinops melanostictus*) larvae based on otolith microstructure analysis. The optimal growth rate for anchovy larvae occurred at 22.0 °C, whereas that for sardine larvae occurred at 16.2 °C. Ambient temperatures have historically fluctuated between these optima, which could lead to contrasting fluctuations in larval growth rates between the two species. This simple mechanism could potentially cause the shifts between the warm anchovy regime and the cool sardine regime in the western North Pacific. Although retrospective analysis suggested synergistic effects of other factors (e.g., trophic interactions and fishing), the optimal growth temperature concept would provide a possible biological mechanism of anchovy and sardine regime shifts.

Résumé : Les oscillations déphasées des populations de l'anchois et de la sardine ont été attribuées aux changements climatiques. Cependant, les mécanismes biologiques qui causent ces alternances d'espèces n'ont pas été élucidés. Nous proposons ici une hypothèse simple de « température optimale de croissance » selon laquelle les changements de régime des anchois et des sardines s'expliquent par des températures optimales différentes pour les taux de croissance durant les premiers stades du cycle. L'analyse de la microstructure des otolithes révèle des relations en forme de dôme entre le taux de croissance et la température de la mer, tant chez les larves de l'anchois japonais (*Engraulis japonicus*) que chez celles de la sardine japonaise (*Sardinops melanostictus*). Le taux optimal de croissance des larves d'anchois se situe à 22,0 °C, alors que celui des larves de sardines est à 16,2 °C. Les températures ambiantes ont fluctué dans le passé entre ces optimums, ce qui a pu établir des fluctuations contrastées des taux de croissance larvaire entre les deux espèces. Ce mécanisme simple peut potentiellement générer des alternances entre le régime chaud des anchois et le régime frais des sardines dans l'ouest du Pacifique Nord. Bien qu'une analyse rétrospective indique des effets de synergie d'autres facteurs (par ex., les interactions trophiques et la pêche), l'hypothèse d'une température optimale de croissance pourrait fournir un mécanisme biologique possible des alternances de régime entre les anchois et les sardines.

[Traduit par la Rédaction]

Introduction

A mystery of the oceans is the phenomenon of out-of-phase population oscillations between species of anchovy and sardine. Dominance in the ocean has historically shifted from anchovy to sardine and back approximately every 50 years on a basin scale (Chavez et al. 2003), with synchronous patterns being observed off Japan, California, Peru, and Chile (Kawasaki 1983; Lluch-Belda et al. 1989; Schwartzlose et al. 1999), but in recent years the sardine stock off California has not exhibited this synchronicity (Bakun and Broad 2003). Enormous efforts through correlative approaches have revealed that these boom-and-bust cycles are associated with long-term atmosphere–ocean state shifts, as climate impacts marine ecosystems (McGowan et al. 1998; Attrill and Power 2002). Thus, these species alternations (fish regime shifts) have been attributed not to overfishing or local events but to climate changes (ocean regime shifts) (Lluch-Belda et al. 1989; McFarlane et al. 2002; Chavez et al. 2003). However, predicting future trends is impossible without first clarifying the underlying processes through mechanistic approaches (Gargett 1997). Despite the

Received 7 May 2006. Accepted 22 March 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 12 June 2007. J19309

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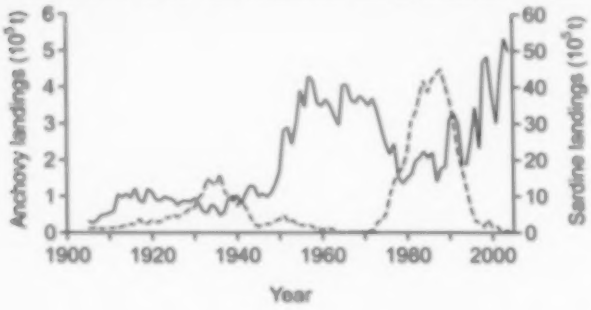
 doi:10.1139/F07-052 © 2007 NRC Canada

Fig. 1. Japanese anchovy (*Engraulis japonicus*, solid line) and Japanese sardine (*Sardinops melanostictus*, broken line) regime shifts recorded in the total commercial landing histories in Japan.



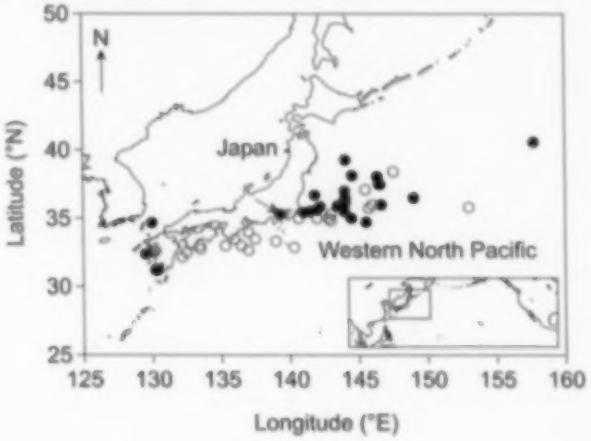
notorious complexity of marine ecosystems, the dominant mechanism responsible for such large-scale events may be relatively simple and direct (Chavez et al. 2003).

Recently, in the western North Pacific, the stock of Japanese sardine (*Sardinops melanostictus*) has almost collapsed, while the stock of Japanese anchovy (*Engraulis japonicus*) has flourished (Fig. 1). The prevailing scenario for Japanese sardine is summarized as the following climate-induced cascade processes. When the wintertime Aleutian low intensifies, the sea temperature at the surface layer falls and the mixed layer becomes deeper in the nursery grounds (Yasuda et al. 1999). These conditions increase the primary production levels and zooplankton biomass (Polovina et al. 1995). The higher food availability presumably enhances larval survival, leading to sardine to flourish (Noto and Yasuda 1999; Yatsu et al. 2005). Conversely, a weakened Aleutian low leads to reduced food supplies and eventually sardine to collapse. Similarly, food-based scenarios focusing on bottom-up control in a climate cascade have been developed for marine ecosystems worldwide (e.g., Cushing 1975; Beaugrand et al. 2003; Ware and Thomson 2005). The existing theories are useful at least as single species scenarios. A crucial missing link, however, is an understanding of the biological processes that govern anchovy and sardine regime shifts.

Two key questions have emerged. As a preliminary query, why do even subtle environmental changes sometimes trigger drastic fish regime shifts? Climate change is undoubtedly influential; however, fish usually experience only relatively subtle environmental changes. Nonetheless, subtleties appear to have major impacts on fish population dynamics. Subsequently, the primary enigma arises. Why do anchovy flourish and sardine collapse simultaneously, or vice versa, under the same ocean regime? It might be logical to assume that one collapses owing to food depletion. However, it remains unclear why its counterpart flourishes despite the same environments and the dominance then alternates abruptly. The existing hypotheses can explain the rise or fall of single species, but have failed to account for the between-species alternation phenomena. Neither density-dependent processes nor between-species competitions fully explain these events.

Initially, we incorporated the growth–survival paradigm — faster-growing fish larvae have a higher probability of survival (Anderson 1988) — into the climate-induced cascade processes to theoretically address the preliminary query. Fish have high mortality rates during early life stages. Growth rates during these stages strongly influence survival and subsequent recruitment success; subtleties in growth rates could lead to dramatic events (Houde 1987, 1989; see also Discussion). We then focus on the direct impacts of sea temperature on larval growth rates.

Fig. 2. Sampling stations for Japanese anchovy (*Engraulis japonicus*, solid circles) and Japanese sardine (*Sardinops melanostictus*, open circles) larvae from 1990 to 2004. The anchovy larvae were collected from April to December; the sardine larvae were collected from January to June. The arrow indicates the coastal station at which both species were repeatedly sampled. Sample profiles are shown in Appendix A.



The present study showed differential optimal temperatures for growth rates during early life stages of Japanese anchovy and Japanese sardine in the western North Pacific, leading to a new hypothesis as a potential biological mechanism of the anchovy and sardine regime shifts. Historical patterns of the temperatures that anchovy and sardine larvae would have experienced were examined, using the long-term data set of the egg and larval surveys, to test the hypothesis based on differential optimal growth temperatures.

Materials and methods

Field sampling

Japanese anchovy and Japanese sardine larvae were collected at a total of 50 stations, ranging from inshore to offshore waters, in the western North Pacific during 1990–2004 (Fig. 2). The larvae were captured mainly by horizontal or oblique tows of various types of trawl and larval and plankton nets at the surface layer; they were frozen at –20 °C or preserved in 80%–90% ethanol immediately after sampling. A total of 34 samples comprising 2041 individuals of anchovy larvae of 6.4–34.3 mm standard length (SL) and 30 samples comprising 766 individuals of sardine larvae of 8.0–33.5 mm SL were used for the subsequent otolith microstructure analysis (Appendix A). The sea surface (0–1 m) temperature (SST) was measured concurrently with larval sampling.

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Otolith microstructure analysis

Daily growth increments on the otoliths of larvae allow their daily growth rate history to be back-calculated based on the close correlation between otolith and somatic sizes (Campana 1990). The SL of each larva was measured to the nearest 0.1 mm. The sagittal otoliths were then dissected from each individual and mounted on a slide glass with enamel resin. We employed an otolith measurement system, which was composed of a transmitted light microscope and video camera connected to a monitor and computer. The maximum otolith radius and each daily growth increment width were measured to the nearest 0.1 μm along a measurement transect set from the nucleus to the outermost margin of the otolith. Although uncoupling between otolith and somatic growth rates could be a possible source of bias in the growth back-calculations (Mosegaard et al. 1988; Hare and Cowen 1995), the otolith radius (x) and SL (y) were highly correlated as allometric relationships for anchovy ($y = 1.544x^{0.539}$, $n = 2041$, $r^2 = 0.932$, $p < 0.001$) and sardine ($y = 2.597x^{0.443}$, $n = 766$, $r^2 = 0.956$, $p < 0.001$) larvae in the present study. Therefore, after determining the allometric relationship between the otolith radius and SL for each larva, the growth rate at each daily age was back-calculated by the biological intercept method (Campana 1990) at the individual level, with the SLs at the first ring deposition (i.e., biological intercepts) fixed at 5.6 mm (4 days old after hatching) for anchovy and 5.0 mm (3 days old after hatching) for sardine. We adopted recent 3-day mean growth rates (mm·day^{-1}) directly before capture to detect the relationship between growth rates and SST at the time of capture (Takasuka and Aoki 2006).

Retrospective analysis

The egg-density-weighted mean SST was calculated separately for anchovy and sardine, based on a long-term data set from the historical records of egg and larval surveys off the Pacific coast of Japan. The survey areas and stations were organized to cover the main coastal spawning grounds for small pelagic fish throughout the year, although they were not perfectly consistent among months or years (Fig. 3). These surveys used a conical or cylindrical–conical plankton net with a 45 or 60 cm diameter and a mesh size of 0.33 or 0.335 mm, which was towed vertically from a depth of 150 m or just above the seabed (<150 m). The updated data set included the results from a total of 102 905 samples of plankton net tows from 1978 to 2004 in conjunction with SST measurements from each towing station. A total of 3188 to 4308 (mean ± standard deviation = 3811 ± 381) samples were available per year, of which 576 to 1485 (925 ± 237) samples included anchovy eggs and 70 to 665 (401 ± 179) samples included sardine eggs. The egg density (number·m^{-2}) was calculated for each tow; the SST was then averaged after being weighted by the egg density over all sampling regions and seasons for each year. We regarded the egg-density-weighted mean SST as a proxy for the ambient temperature that the larvae would have most likely experienced after hatching, in light of spatial and temporal dynamics of the spawning grounds. Larval growth rates were predicted simply from the annual egg-density-weighted mean SSTs, using the relationships between growth rates and SSTs obtained in the field. This solution would allow the relative changes of growth rates to be described, although the absolute values must be treated with caution because of possible nonlinear temperature effects on growth rates. Total commercial catch history data for anchovy and sardine were updated from Yatsu et al. (2005). The time-series data of the growth rates converted from SSTs were compared with those of larval survival and population dynamics. Recruitment per spawning biomass (RPS) was adopted as a larval survival index (but early juveniles were also included). The RPS data, which were calculated as the number of young-of-the-year recruits (0+ year old) divided by the spawning stock biomass (kg) based on the virtual population analyses (Pope 1972), as well as the estimated total biomass data, were derived from the annual stock assessment reports for the Pacific stocks off Japan (Nishida 2005; Oozeki et al. 2005).

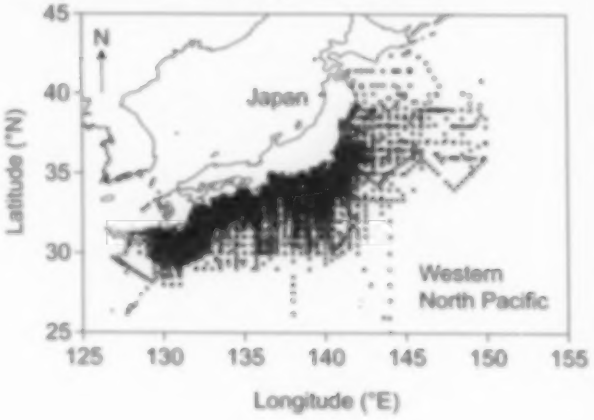

Fig. 3. Sampling stations for Japanese anchovy (*Engraulis japonicus*) and Japanese sardine (*Sardinops melanostictus*) eggs in the egg and larval surveys off the Pacific coast of Japan from 1978 to 2004. All sampling stations, including both fixed and unfixed stations, are collectively shown as crosses.

Results

Systematic patterns were observed between the recent 3-day mean growth rates directly before capture and SST at the time of capture for both anchovy and sardine larvae, even though the larvae were collected from different regions, seasons, and years. The growth rates of the anchovy larvae increased with the SST until they reached a maximum, after which the growth rates decreased as the SST increased (Fig. 4). A dome-shaped relationship was detected between growth rates and SST in the range of 14.0–26.7 °C. From a simple quadratic function fitted to the mean values of growth rates at the sample level, the maximum value of the growth rate of larval anchovy was expected to occur at 22.0 °C ($y = -2.302 + 0.255x - 0.006x^2$, $n = 34$, $r^2 = 0.507$, $p < 0.001$). Similarly, the sardine larvae showed a dome-shaped relationship between growth rates and SST in the range of 11.8–20.2 °C. However, the maximum value of the growth rate of larval sardine was detected at 16.2 °C by a quadratic function ($y = -3.742 + 0.523x - 0.016x^2$, $n = 30$, $r^2 = 0.526$, $p < 0.001$). The difference in the tempera-

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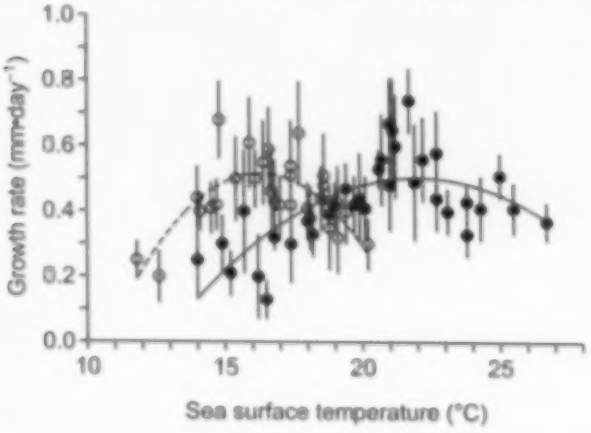
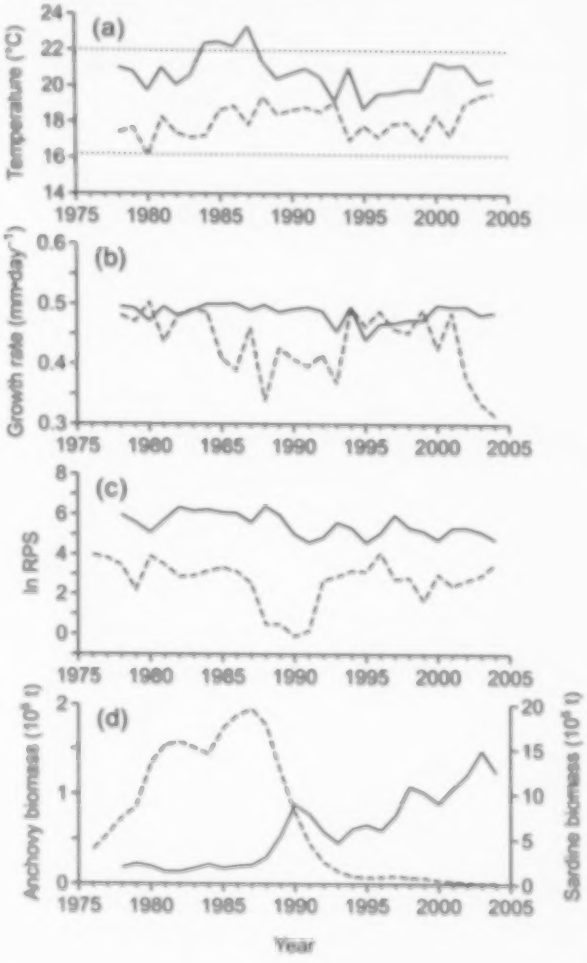
Fig. 4. Relationships between the recent 3-day mean growth rate and the sea surface temperature for larval Japanese anchovy (*Engraulis japonicus*, solid circles) (34 samples comprising 2041 individuals) and larval Japanese sardine (*Sardinops melanostictus*, open circles) (30 samples comprising 766 individuals). Mean ± standard deviation data and quadratic functions fitted to the mean values at the sample level are shown. Anchovy larvae (solid line curve): $y = -2.302 + 0.255x - 0.006x^2$ ($n = 34$, $r^2 = 0.507$, $p < 0.001$); sardine larvae (broken line curve): $y = -3.742 + 0.523x - 0.016x^2$ ($n = 30$, $r^2 = 0.526$, $p < 0.001$).



tures producing maximum values of growth rates between anchovy and sardine larvae was ~6 °C. In addition, comparison of the quadratic curves indicated that the increase or decrease of growth rates with SST shifts was greater for sardine larvae than for anchovy larvae.

The egg-density-weighted mean SSTs for anchovy were consistently higher than those for sardine from 1978 to 2004, with the difference up to 5.5 °C (Fig. 5*a*). However, both of the egg-density-weighted mean SSTs for anchovy and sardine have fluctuated mainly between 16 and 22 °C. Growth rates, which were converted from the egg-density-weighted mean SSTs using the quadratic functions fitted to the growth rates versus SSTs (Fig. 4), showed contrasting fluctuations between these two species (Fig. 5*b*). The converted growth rates of the sardine larvae markedly declined in the mid-1980s and continued to be at a low level for a decade until recovery, while the converted growth rates of the anchovy larvae were relatively stable at a high level during that period. Conversely, the growth rates of the sardine larvae increased and those of the anchovy larvae slightly decreased simultaneously around the mid-1990s. The RPS generally showed similar patterns in their temporal shifts with the converted growth rates, although the declines before the late 1980s and in recent years were observed in the growth rates but not in the RPS for sardine and yearly correspondences seemed ambiguous for anchovy (Fig. 5*c*). The relationship between the converted growth rates and lnRPS was significant for sardine during 1978–2000 (Spearman's correlation coefficient test, $n = 23$, $r = 0.437$, $p < 0.05$), although the relationship during 1978–2004 was not significant for sardine ($n = 27$, $r = 0.226$, $p > 0.05$) or anchovy ($n = 27$, $r = 0.347$, $p > 0.05$). The drastic decline of the sardine biomass occurred in the late 1980s, after which

Fig. 5. Retrospective analysis to examine the relationship among time-series data of temperature, growth rate, survival index, and biomass for Japanese anchovy (*Engraulis japonicus*, solid line) and Japanese sardine (*Sardinops melanostictus*, broken line). (*a*) Egg-density-weighted mean sea surface temperature (SST; °C) as a proxy for temperatures in the spawning grounds. Dotted lines indicate the optimal growth temperatures for anchovy (22.0 °C) and sardine (16.2 °C) larvae. (*b*) Larval growth rate (mm·day^{-1}) converted from the egg-density-weighted mean SST using the growth–temperature relationship in Fig. 4. (*c*) Ln-transformed recruitment per spawning biomass (RPS; number·kg^{-1}) as a proxy for larval survival. (*d*) Biomass (t) of the Pacific stocks off Japan. RPS (*c*) and biomass (*d*) data originated from the same data set in the annual stock assessment reports for the Pacific stocks off Japan.



their biomass continued to be at the low level and has not yet recovered (Fig. 5*d*). In contrast, the anchovy biomass started to increase in the late 1980s and continued to increase gradually (but with slight and episodic declines in the mid-1990s) during the same period. The ratio of the biomass in a year to that of the previous year was significantly related with the lnRPS of the previous year for anchovy during 1979–2004

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($n = 26$, $r = 0.517$, $p < 0.01$) and for sardine during 1977–2004 ($n = 28$, $r = 0.714$, $p < 0.001$). The extent of the biomass fluctuations for sardine (maximum/minimum = 190) was far greater than that for anchovy (maximum/minimum = 11).

Discussion

Here we propose the "optimal growth temperature" hypothesis as a potential biological mechanism for anchovy and sardine regime shifts. Through otolith microstructure analysis, we demonstrated differential optimal temperatures for growth rates during early life stages of Japanese anchovy (22.0 °C) and Japanese sardine (16.2 °C) in the western North Pacific. Dome-shaped relationships were detected between growth rates and temperatures for both anchovy and sardine larvae. This indicates the existence of an optimal temperature for larval growth rates within the large temporal and spatial scales experienced in the field (Brett 1979; Buckley et al. 2004; Takasuka and Aoki 2006). Elevated temperatures promote somatic growth up to a certain point, above which growth declines owing to the excessive metabolic rate induced by hyperoptimal temperatures (Brett 1979). In the western North Pacific, the warm anchovy regime has historically shifted to the cool sardine regime and back (Chavez et al. 2003). If these species experience similar conditions, the differential optimal temperatures for larval growth rates would explain such fish regime shift phenomena theoretically (Fig. 6). When the temperature is around 22 °C, the growth rates of anchovy larvae will be at the maximum level, while those of sardine larvae will, by extrapolation, be at the minimum level. Therefore, the anchovy will flourish and the sardine will collapse simultaneously, according to the growth–survival paradigm. As the ocean regime shifts and the temperature declines, the anchovy growth rates will decrease gradually, while the sardine growth rates will increase rapidly. When the temperature reaches around 16 °C, the anchovy will collapse and sardine will flourish. If the temperature turns back with the next ocean regime shift, the fish regime will do the same. The temperature shifts between these optima would simply explain the shifts from the dominance of one species to the other and back. That is the conceptual framework of a potential biological mechanism of fish regime shifts by differential optimal growth temperatures during early life stages.

However, in reality, anchovy and sardine do not always experience the same environments; sardine spawn earlier, with the peak over a more restricted period in early spring, than anchovy, with the peak extending from spring to summer. So, what temperatures do these larvae experience? Although the anchovy larvae would have encountered higher temperatures than the sardine larvae, the ambient temperatures for both larvae fluctuated mainly between their optimal growth temperatures. As such, the growth rates indicated contrasting fluctuations between the two species, and these patterns seemed consistent with the temporal shifts of RPS and biomasses for the phase of the drastic alternation from sardine to anchovy, although discrepancies were partly observed among time-series data for some periods. In the North Pacific, the ocean regime shift occurred in the late 1980s (Hare and Mantua 2000). The sardine larvae would have sustained higher growth rates before the late 1980s, and thus the sardine biomass would have increased until that time. However, the growth rates of the sardine larvae would have then declined, owing to the hyperoptimal temperatures. This timing roughly corresponded to the crucial RPS declines and the beginning of the population collapse of the sardine. In contrast, the growth rates of the anchovy larvae would not have declined under the same ocean regime, which probably led to the increasing anchovy biomass. That is, we consider, why anchovy flourish and sardine collapse or vice versa under the same ocean regime. In addition, the difference in the extent of biomass fluctuations might be related to the fact that sardine growth rates responded to temperature shifts more markedly than anchovy growth rates.

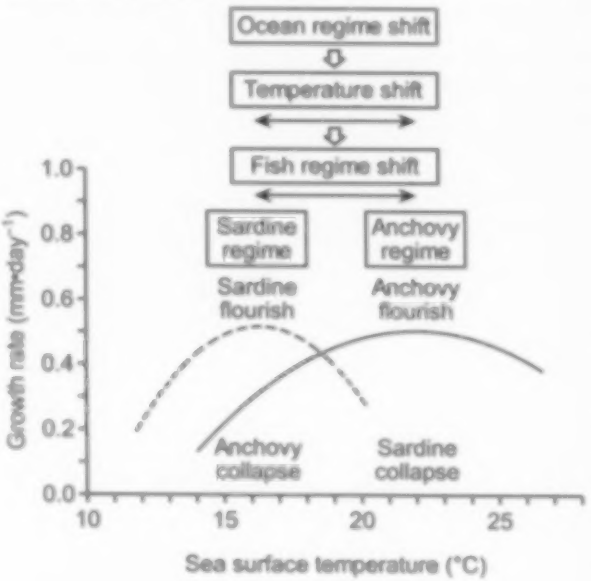

Fig. 6. Conceptual framework of the optimal growth temperature hypothesis: a potential biological mechanism for the anchovy and sardine regime shifts under the assumption that both types of larvae experience similar temperatures during the same period. Quadratic functions for Japanese anchovy (*Engraulis japonicus*, solid curve) and Japanese sardine (*Sardinops melanostictus*, broken curve) were derived from Fig. 4.

The optimal growth temperature hypothesis assumes that even subtle growth variations driven by subtle temperature shifts could potentially cause drastic fish regime shifts. The growth–survival paradigm includes three functional mechanisms in its theoretical framework (Takasuka et al. 2004*a*). Higher growth rates enhance larval survival through the indirect advantages of larger body size (the bigger-is-better hypothesis; Miller et al. 1988) and the shorter high-mortality larval stage (the stage duration hypothesis; Houde 1987, 1989). Moreover, growth rates directly impact predation mortality; faster-growing larvae are less vulnerable to predation (the growth-selective predation hypothesis; Takasuka et al. 2003, 2004*b*). A simulation study (Houde 1987) showed that greater than hundredfold differences in larval survival could be derived from growth variability through the stage

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duration mechanism. The growth-related mechanisms can serve as an amplifier.

The retrospective analysis indicated both positive and negative aspects of the optimal growth temperature hypothesis, providing perspectives on the role of mechanism. The present hypothesis was tentatively supported for the phases of the drastic shift from sardine to anchovy. Yet discrepancies were observed among the time-series data during some phases. For example, the higher growth rates and RPSs in the mid-1990s did not allow the sardine population to recover. This is probably because of adverse circumstances due to compounding effects of multiple factors. In particular, fishing pressure could prevent stock recovery when the spawning biomass was too low (Hutchings 2000; Shelton et al. 2006). Also, some gaps were observed in trends between growth rate and RPS series, maybe partly owing to potential problems in power of the indices (Cardinale and Hjelm 2006). In any case, aspects not in agreement with the optimal growth temperature hypothesis suggested the potential effects of the other factors. Undoubtedly, no single factor is enough to explain the whole picture of fish population dynamics in light of the complexity of marine ecosystems (e.g., Duffy-Anderson et al. 2005). In theory, the optimal growth temperature hypothesis is independent of and synergistic with existing hypotheses. Thus, its ramifications could be multiplied, mitigated, or masked by food-related pathways (bottom-up controls) (Beaugrand et al. 2003; Platt et al. 2003; Ware and Thomson 2005), predator fields (top-down controls) (Frank et al. 2005), interactions among species (Bakun and Cury 1999; Bakun and Broad 2003; Alheit and Niquen 2004), physical factors (such as wind, current flow, and upwelling; MacCall 2002; Cury and Roy 1989), and human impacts (such as fishing; Cury and Shannon 2004). Here, we nonetheless intentionally focused on a single factor, temperature, to extract a new concept to explain the species alternations under the same ocean regime. In a sense, the temperature shifts might provide necessary conditions rather than being the sole condition to initiate fish regime shifts. The simple and direct optimal growth temperature hypothesis is a potential biological mechanism for the alternation phases that have not been addressed by the existing mechanisms. The present hypothesis extended the optimal environmental window theory (Cury and Roy 1989), which focused on the moderate upwelling intensity favorable for recruitment, to the multispecies alternation phenomena. The growth–survival paradigm, direct temperature impacts, and differential optimal growth temperatures constitute the bottom line of our concept.

A further question is why fish regime shifts were synchronous despite the reversed sea temperature regimes between the opposite sides of the Pacific in the past (MacCall 2002; Bakun and Broad 2003; Chavez et al. 2003). This synchronicity is possibly because optimal temperatures of anchovy and sardine are reversed across the Pacific. In fact, northern anchovy (*Engraulis mordax*) showed a spawning peak at 14 °C as a cool and stenothermal species, while California sardine (*Sardinops sagax*) showed peaks at 15 and 23 °C as a warm and eurythermal species in the California Current system (Lluch-Belda et al. 1991), in contrast with the anchovy (*E. japonicus*) and sardine (*S. melanostictus*) in the western North Pacific. In terms of temperature optima, the anchovy and sardine relationships are reversed across the North Pacific. The optimal growth temperature hypothesis may also bear generality and applicability to basin-scale phenomena.

Escalating global warming is jeopardizing the future of marine organisms (Levitus et al. 2000). Fish might migrate to more favourable habitats, but they will not avoid basin-wide warming in the long term. Even a 2–3 °C rise of SST due to global warming during the next century could exert severe impacts on fish regimes. If so, the ongoing fish regime shift itself might collapse, as the sardine will face crisis earlier than the anchovy, leading to a permanent regime or another less welcome state in the western North Pacific.

Acknowledgements

We thank T. Yamakawa, H. Sugisaki, H. Saito, and Y. Kurita for their critical and constructive comments on the earlier drafts. The otolith data were supplemented by H. Kubota (six anchovy samples), R. Kimura (seven sardine samples), and H. Sugisaki (three sardine samples). The present study benefited from discussions with T. Akamine, J. Alheit, A. Bakun, Y. Ishida, H. Kubota, K. Nakata, H. Nishida, M. Noto, R.H. Parrish, H. Saito, H. Sugisaki, Y. Tsuruta, T. Yamakawa, Y. Yamashita, I. Yasuda, and A. Yatsu. The field sampling and data collection were supported by a multitude of officers, crew, fishery operators, and participating researchers. We also thank D. Welch and one anonymous reviewer for helpful advice that greatly improved the manuscript.

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Appendix A

Table A1. Information on Japanese anchovy (*Engraulis japonicus*) and Japanese sardine (*Sardinops melanostictus*) larval samples used for otolith microstructure analysis.

Sample No.	Date	Latitude (°N)	Longitude (°E)	SST (°C)	*n*	SL (mm)
Anchovy						
A-01	15 Aug. 1996	40°35′	157°45′	19.7	51	10.9–32.7
A-02	17 Aug. 1996	39°17′	144°04′	23.8	19	12.0–18.2
A-03	11 June 1997	35°00′	144°30′	20.7	100	13.1–31.1
A-04	13 June 1997	36°42′	141°50′	20.6	60	14.6–25.7
A-05	22 May 1999	35°30′	143°59′	21.1	8	15.4–22.0
A-06	2 June 1999	36°30′	149°01′	21.2	7	10.4–17.6
A-07	7 Apr. 2000	35°26′	141°02′	15.7	110	8.9–31.4
A-08	7 Apr. 2000	35°31′	141°30′	16.2	27	7.5–21.2
A-09	7 Apr. 2000	35°37′	141°59′	16.5	32	6.8–19.2
A-10	7 Apr. 2000	35°55′	143°29′	14.9	93	9.6–26.4
A-11	7 Apr. 2000	36°00′	144°00′	14.0	17	10.4–26.5
A-12	8 Apr. 2000	36°21′	144°00′	17.4	109	6.4–27.1
A-13	8 Apr. 2000	37°00′	144°00′	15.2	14	7.8–16.1
A-14	15 May 2000	38°08′	144°34′	19.4	47	14.4–27.4
A-15	28 Oct. 2000	35°18′	139°21′	21.0	60	14.0–30.0
A-16	3 Nov. 2000	35°18′	139°21′	20.1	60	15.2–24.8
A-17	23 Nov. 2000	35°18′	139°21′	18.2	120	18.7–28.6
A-18	12 May 2001	36°00′	146°40′	21.0	69	12.6–26.4
A-19	25 May 2001	31°13′	130°15′	23.8	12	17.3–20.7
A-20	25 May 2001	31°12′	130°23′	24.3	7	14.3–21.2
A-21	1 July 2001	35°18′	139°21′	22.7	60	15.9–30.1
A-22	5 July 2001	35°18′	139°21′	23.1	60	15.6–33.2
A-23	18 July 2001	35°18′	139°21′	25.5	120	16.1–32.4
A-24	8 Nov. 2001	35°18′	139°21′	19.0	120	20.4–31.4
A-25	31 May 2002	35°52′	142°13′	22.7	84	7.6–23.1
A-26	2 June 2002	34°43′	145°34′	22.2	178	7.4–30.5
A-27	5 June 2002	37°30′	146°30′	21.7	15	26.4–34.3
A-28	6 June 2002	37°30′	146°35′	19.9	128	10.3–31.0
A-29	7 June 2002	38°03′	146°23′	21.9	141	9.3–34.0
A-30	2 Sept. 2002	32°22′	129°33′	26.7	12	14.9–17.8
A-31	14 Sept. 2002	34°40′	130°00′	25.0	25	17.0–24.0
A-32	25 Nov. 2003	35°18′	139°21′	18.8	25	18.0–26.3
A-33	5 Dec. 2003	35°18′	139°21′	18.0	26	19.3–29.0
A-34	15 Dec. 2003	35°18′	139°21′	16.8	25	20.0–30.3
Sardine						
S-01	25 Feb. 1990	33°00′	133°30′	17.7	16	8.5–15.5
S-02	26 Feb. 1990	32°45′	133°30′	18.1	11	8.9–13.6
S-03	20 Feb. 1992	33°30′	137°30′	19.4	11	8.0–13.2
S-04	23 Feb. 1992	33°00′	136°30′	19.1	13	8.2–15.3
S-05	28 Feb. 1992	32°30′	132°30′	18.6	48	9.8–18.5
S-06	10 Apr. 1992	34°50′	143°00′	18.0	14	13.2–17.0
S-07	6 May 1992	35°50′	153°00′	14.1	15	26.8–33.5
S-08	10 Feb. 1993	33°20′	139°00′	20.2	18	8.0–10.5
S-09	13 Feb. 1993	34°00′	137°00′	18.6	40	8.0–18.2
S-10	16 Feb. 1993	32°40′	137°00′	19.1	43	8.0–13.7
S-11	18 Feb. 1993	33°29′	136°01′	18.5	23	8.0–14.8

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Table A1 (*concluded*).

Sample No.	Date	Latitude (°N)	Longitude (°E)	SST (°C)	*n*	SL (mm)
S-12	25 Feb. 1993	35°00′	140°39′	16.7	52	8.3–16.6
S-13	26 Feb. 1993	35°00′	142°00′	18.8	44	8.1–16.6
S-14	27 Feb. 1993	35°19′	143°00′	17.4	51	9.0–18.1
S-15	2 Mar. 1993	33°00′	135°20′	16.8	17	8.5–14.3
S-16	4 Mar. 1993	32°53′	140°20′	18.8	50	8.4–24.5
S-17	5 Mar. 1993	32°10′	132°10′	17.0	15	8.3–15.2
S-18	5 Mar. 1994	35°00′	142°50′	14.8	23	15.1–22.8
S-19	11 May 1996	35°45′	145°45′	17.4	12	16.8–25.0
S-20	12 May 1996	36°00′	146°00′	16.6	9	20.9–25.6
S-21	18 May 1996	37°07′	145°30′	16.1	9	13.8–23.1
S-22	19 May 1996	36°20′	144°00′	15.4	25	16.7–23.7
S-23	19 May 1996	36°27′	144°03′	15.9	16	16.5–21.1
S-24	20 May 1996	36°15′	144°01′	16.4	10	16.1–21.3
S-25	4 June 1997	38°26′	147°33′	17.4	39	23.2–30.4
S-26	20 Jan. 2004	35°18′	139°21′	14.0	30	20.9–30.8
S-27	26 Jan. 2004	35°18′	139°21′	14.7	43	20.8–29.7
S-28	30 Jan. 2004	35°18′	139°21′	14.5	23	18.6–33.4
S-29	16 Feb. 2004	35°18′	139°21′	11.8	20	21.6–31.6
S-30	25 Feb. 2004	35°18′	139°21′	12.6	26	22.1–29.7

Note: SST, sea surface temperature; SL, standard length.

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Hierarchical analysis of relationships between brook trout (*Salvelinus fontinalis*) density and stream habitat features

Julie Deschênes and Marco A. Rodríguez

Abstract: We used hierarchical linear regression to examine relationships between brook trout (*Salvelinus fontinalis*) density and habitat features nested at three levels: sections within reaches, reaches within streams, and streams within a basin. Brook trout density and environmental variables were quantified at 600 stream sections distributed among 120 reaches and 22 streams in the Cascapedia River basin, Quebec, Canada. Decomposition of variance showed that variation in density among streams was small relative to that among sections or reaches and not statistically significant. Density was influenced by habitat variables at both the section (current velocity, woody debris, cover) and reach (subbasin area, height increment at flood, valley width) levels. A cross-level interaction between current velocity and subbasin area pointed to a "contextual" effect: density showed stronger decline with current velocity in larger subbasins than in smaller subbasins. This result suggests that there was no single "best scale" for examining fish–environment relationships. Accounting for contextual effects by use of hierarchical models can enhance our understanding of how habitat features influence fish densities at multiple spatial scales.

Résumé : La régression linéaire hiérarchique nous a permis d'examiner les relations entre la densité d'ombles de fontaine (*Salvelinus fontinalis*) et les caractéristiques environnementales emboîtées à trois niveaux hiérarchiques : les sections à l'intérieur des tronçons, les tronçons à l'intérieur des tributaires et les tributaires à l'intérieur d'un bassin. Nous avons échantillonné les poissons et les variables environnementales dans 600 sections réparties sur 120 tronçons et 22 tributaires de la rivière Cascapédia (Québec), Canada. La décomposition de la variance montrait que la variation de la densité entre tributaires n'était pas significative et était plus faible que celle entre sections ou entre tronçons. La densité était influencée par des caractéristiques environnementales aux niveaux des sections (vitesse du courant, débris ligneux, couvert) et des tronçons (superficie du sous-bassin, augmentation de la hauteur à la crue, largeur de la vallée). L'interaction entre la vitesse du courant et la superficie du sous-bassin suggérait l'existence d'un effet contextuel : l'influence négative de la vitesse du courant sur la densité était plus forte dans les grands sous-bassins que dans les petits sous-bassins. Les résultats indiquent qu'il n'y avait pas d'échelle « optimale » pour l'analyse des rélations poissons–environnement. L'examen des effets contextuels à l'aide des modèles hiérarchiques peut améliorer notre compréhension des relations poissons–environnement à plusieurs échelles spatiales.

Introduction

Ecological data often have clustered or nested structure that arises from observations made on sampling units grouped at different hierarchical levels. Because sampling levels can be chosen to correspond to spatial scales of analysis, nested sampling designs can be useful in examining fish–habitat relationships at multiple spatial scales. The hierarchical structure in data from such designs can be exploited to address questions about the scale dependence of patterns and responses, e.g., do environmental features influence fish distribution similarly across channel units nested within reaches, reaches nested within streams, or streams nested within a basin? (Dunham and Vinyard 1997; Inoue et al. 1997; Watson and Hillman 1997).

By explicitly considering hierarchical structure, one can also examine potential "cross-level" interactions between environmental variables characterising units at different spatial scales. Such interactions may result in contextual effects in which the influence of a local environmental variable is contingent upon the level of another, larger-scale variable. For example, in Japanese streams, the influence of cover on the abundance of masu salmon (*Oncorhyncus masou*) within a small-scale channel unit (pool, riffle, glide, cascade, or rapid) differs across large-scale geomorphic channel types comprising groups of 60 to 70 channel units (Inoue et al. 1997). At the scale of a pool–riffle sequence, salmon density is positively related to the abundance of cover, but at the scale of stream reaches (10 pool–riffle sequences), this relationship only holds when cover is rare (Inoue et al. 1997).

Received 7 July 2006. Accepted 26 March 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 12 June 2007. J19405

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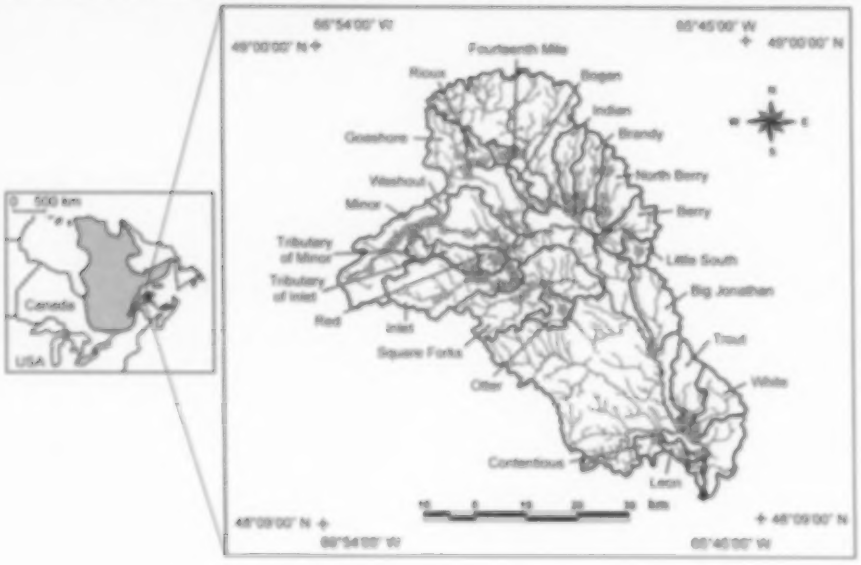
 doi:10.1139/F07-053 © 2007 NRC Canada

Fig. 1. Location of the 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin, Québec, Canada.



Patterns and processes detected at local spatial scales do not necessarily also apply at larger scales (Inoue et al. 1997; Folt et al. 1998; Schneider 2001). Examples of apparent inconsistencies in patterns and processes across scales include differences in habitat preference of fish species across river sections or reaches (Poizat and Pont 1996), fish response to environmental features across basins (Dunham and Vinyard 1997; Watson and Hillman 1997), and longitudinal distribution of mesohabitats across hydro-ecoregions (Cohen et al. 1998). These examples hint at potential outcomes of cross-level interactions and suggest that the above inconsistencies may be resolved by explicitly considering such interactions.

Nested sampling designs can yield useful insights into processes operating at multiple spatial scales, yet few studies in stream ecology seem to have fully exploited this potential. One technical obstacle has been that in nested samples, units within a group usually tend to be more similar to other units within their group than to units in other groups. Thus, individual observations are not entirely independent as required by conventional regression models.

This potential drawback is addressed by hierarchical regression modelling, a statistical approach that copes effectively with nested data structures and allows for inclusion of effects operating at several levels, as well as cross-level interactions, in a single model (Hox 2002; Goldstein 2003). In this study, we use hierarchical linear (HL) regression to examine the relationships between brook trout (*Salvelinus fontinalis*) density and environmental features nested at three spatial scales: across sections within reaches and streams, across reaches within streams, and across streams within a basin.

Materials and methods

Fish sampling and environmental measurements

Brook trout density and environmental variables were quantified at 600 sections distributed among 120 sampling sites and 22 tributary streams in the Cascapedia River basin (3179 km^2), Québec, Canada (Fig. 1). Sites were selected to maximize spatial coverage of the basin subject to accessibility constraints. Sites were visited in random sequence during low flow from mid-June to late August in 2000 (24 sites), 2001 (48 sites), and 2002 (48 sites). At each site, samples were collected from a 75-m stream reach comprising five adjacent sections, each approximately 15 m in length. No attempt was made to position sampled reaches to coincide with habitat boundaries. The nested sampling design therefore spanned three spatial scales: sections within reaches (maximum fluvial distance between sections = 0.075 km), reaches within streams (maximum fluvial distance between reaches averaged across streams = 8 km), and streams within the basin (maximum fluvial distance between stream mouths = 82 km).

Sampled areas covered the entire stream width in completely wadable reaches and ranged 5 m from one bank, chosen randomly, towards the opposite bank otherwise. Fish were sampled by single-pass electrofishing (Smith-Root D-15) in an upstream direction within open stream sections (Lobón-Cerviá and Utrilla 1993; Crozier and Kennedy 1994; Jones and Stockwell 1995). All captured fish were identified, measured, weighed, and returned to their point of capture. Brook trout density was calculated as total captures divided by section area (numbers·100 m^{-2}). Because capture efficiency is not 100%, this measure underestimates true density but should be proportional to it if efficiency is comparable across sampling units, an assumption that seems tenable given that all sites were sampled under base flow conditions.

In all, 21 environmental variables were quantified at the section, reach, or stream scales (Table 1). For each section, water depth and substratum size (modified Wentworth scale) were measured at five equidistant points along each of four equidistant transects perpendicular to stream flow. Current

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Table 1. Hierarchical level (HL), median, and quartiles (25%–75%) for 21 environmental variables describing fish habitat in 600 sections distributed among 120 reaches and 22 streams of the Cascapedia River basin.

Variable name	HL	Median	Quartiles (25%–75%)
Overhead opening (°)	Section	95.7	75.4–113.5
Cover index	Section	2.4	1.4–3.0
Mean depth (cm)	Section	24.6	18.8–29.4
Mean current velocity ($cm \cdot s^{-1}$)	Section	34.9	26.0–48.9
Mean substratum size index	Section	5.3	4.9–5.8
Mean wetted width (m)	Section	9.3	6.3–14.1
Large woody debris (number)	Section	3.5	1.0–8.5
Vegetation abundance index	Section	1.0	1.0–1.8
Accessibility index	Reach	0.8	0.3–1.0
Altitude (m)	Reach	240.0	167.5–315.0
Distance to mainstem (km)	Reach	9.1	2.5–21.7
Entrenchment (%)	Reach	10.0	5.0–15.0
Height increment at flood (m)	Reach	0.5	0.4–0.7
Mean temperature (°C)	Reach	10.5	9.0–12.0
Stream slope (°)	Reach	1.0	0.6–1.3
Stream gradient (°)	Reach	2.1	0.6–3.3
Stream order	Reach	3.0	3.0–4.0
Valley width (m)	Reach	180.0	95–350
Subbasin area (km^2)	Reach	70.1	25.5–151.0
Width increment at flood[a] (m)	Reach	2.6	1.9–4.0
Distance to mouth (km)	Stream	75.5	52.8–82.4

Note: The hierarchical level indicates the scale at which measurements varied among sampling units.
[a]Sum of measures from right and left margins.

velocity (pygmy-type meter, Scientific Instruments 1205) was measured at five equidistant points along the second transect from the downstream end. Wetted width was measured at each transect. Abundance of submerged vegetation (moss or macrophytes) and overall availability of structural cover (rocks, woody debris, undercut bank, and overhanging vegetation) were estimated visually and assigned ordinal values reflecting areal coverage (1, ≤5%; 2, 6%–15%; 3, 16%–45%; 4, >45%). Overhead opening (angle between riparian canopy or hilltops blocking incident sunlight at the centre of the stream; Table 1) and slope over the stream reach were measured with a handheld clinometer (Suunto MP-5). The increment in stream height and width at flood (from annual flood marks) were measured on site for each section and averaged by reach. Water temperature was measured at each section (handheld thermometer, Barigo). Entrenchment (mean gradient ≤100 m away from stream bank), valley width (distance between piedmonts on each side of the stream), stream order (Strahler scale), and altitude were obtained from 1:20 000 topographic maps, as were distances by waterway from each section to the Cascapedia River ("distance to mainstem") and from the mouth of each stream to the mouth of the Cascapedia River ("distance to mouth") (planimeter, Calculated Industries 6125). Subbasin surface area and stream gradient (mean slope from sampling reach to source) were obtained from 1:20 000 maps (Ministère des Ressources naturelles du Québec) by use of a geographic information system (ArcView 3.2, ESRI, Redlands, Calif.). Units of large woody debris (>10 cm diameter) and pools were counted within each section. Physical barriers potentially affecting upstream migration of fish along a tributary were assessed from field observations and topographic maps, and their effectiveness was coded as an integer value, B, ranging from 0 (no visible barrier) to 4 (insurmountable barrier), reflecting the height, type (beaver dams, log jams, culverts, falls), and configuration of the barrier. An index of accessibility combining multiplicatively all potential barriers for each site was calculated:

$$\text{accessibility} = \prod_{i=1}^{N}\left(1 - \frac{B_i}{4}\right)$$

where N is the number of visible barriers and B_i is the effectiveness of barrier i downstream from the site. Accessibility was assigned the value 1 in the absence of visible barriers. The index thus ranged from 0 to 1, taking a value of 0 if at least one barrier was insurmountable ($B_i = 4$).

Quantitative analyses

The relationships between brook trout density and habitat features nested at different hierarchical levels were examined by use of HL regression (program MLwiN, version 2.0; Rasbash et al. 2004), a model known as linear mixed effects in the statistical literature and multilevel regression in the social sciences. The description that follows is largely drawn from Hox (2002) and Goldstein (2003). The HL model relates observations made on I units clustered within J groups to one or more predictor variables (X_{ij}). For a single predictor,

$$Y_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + \varepsilon_{ij}$$

where β_{0j} is the intercept and β_{1j} is the group-specific slope for the predictor. Departure of observation i from the predicted regression line of group j is represented by the

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random term ε_{ij}, the level-one residuals. In contrast to ordinary least-squares (OLS) regression, HL regression assumes that groups are randomly sampled from a larger population of groups, and sampling units within groups need not be independent. Variation among groups in the intercept β_{0j} and slope β_{1j} is characterized as

$$\beta_{0j} = \beta_0 + u_{0j}$$

$$\beta_{1j} = \beta_1 + u_{1j}$$

where the random effects u_{0j} and u_{1j} represent departures of the intercept and slope of group j from the fixed terms β_0 (overall mean intercept) and β_1 (overall mean slope), respectively. The random effects u_{0j} and u_{1j}, which represent level-two residuals, explicitly allow for the hierarchical structure of the data and constitute a fundamental difference between OLS and HL regressions. The terms u_{0j}, u_{1j}, and ε_{ij} are assumed to follow normal distributions with zero mean and variances to be estimated ($\sigma^2_{u_0}$, $\sigma^2_{u_1}$, and σ^2_ε). The random effects u_{0j} and u_{1j} are assumed to be independent from the level-one residuals ε_{ij} but generally not from each other.

The intercepts and slopes of the HL regression are weighted averages of OLS estimates for each group and the overall regression estimate for all similar groups. As a result, residuals are shrunken back towards the overall mean. The amount of shrinkage depends on the reliability of the estimate for a group, which is determined by the number of units within the group and the difference between the estimate for the group and the overall mean. Therefore, less reliable estimates are shrunken closer to the mean.

Among-group variation in both intercept and slope can be accounted for by introducing level-two predictors (Z_j):

$$\beta_{0j} = \beta_0 + \beta_{01} Z_j + u_{0j}$$

$$\beta_{1j} = \beta_1 + \beta_{11} Z_j + u_{1j}$$

The full model, including fixed and random terms, is then

$$Y_{ij} = \beta_0 + \beta_1 X_{ij} + \beta_{01} Z_j + \beta_{11} X_{ij} Z_j + u_{0j} + u_{1j} X_{ij} + \varepsilon_{ij}$$

where $X_{ij}Z_j$ is a cross-level interaction between level-one and level-two predictors.

The regression model was produced by a forward selection procedure in which individual terms were selected according to the significance of changes in deviance between models (log-likelihood ratio tests, $\alpha = 0.05$). A stepwise sequence similar to that proposed by Hox (2002) was followed in building the final model. In the first step, the total variance in brook trout density was decomposed and apportioned among hierarchical levels by use of the classical model for variance components:

$$Y_{ijk} = \beta_0 + u_{0jk} + v_{0k} + \varepsilon_{ijk}$$

where $u_{0jk} \sim N(0, \sigma^2_{u_0})$, $v_{0k} \sim N(0, \sigma^2_{v_0})$, and $\varepsilon_{ijk} \sim N(0, \sigma^2_\varepsilon)$ and the σ^2 terms represent variances at the stream ($\sigma^2_{v_0}$), reach ($\sigma^2_{u_0}$), and section (σ^2_ε) levels. To determine whether random intercepts were needed at the reach and stream levels, we examined whether brook trout density varied significantly at those levels by using one-sided tests for the corresponding variance terms (Snijders and Bosker 1999; Hox 2002). Because brook trout density did not vary significantly at the highest level, across streams (Table 2), only two-level models reflecting variation at the section and reach levels were considered in subsequent analyses. In the second step, section-level (level-one) predictors were tested one at a time, and the predictor accounting for the greatest change in deviance was added to the model if the change in deviance was significant. This procedure was repeated until no significant reduction in deviance could be attained by including any of the remaining potential predictors. In the third step, the slope coefficients of the selected predictors were tested for significant reach-level (level-two) variation to determine whether random slopes were required for those predictors. In the fourth step, reach-level predictors were tested similarly to the section-level predictors in step 2. In the fifth step, all first-order interaction terms between section- and reach-level predictors already in the model were tested and included in the model if significant.

Table 2. Random-effects decomposition of the total variance in brook trout (*Salvelinus fontinalis*) density, by hierarchical level (HL).

HL	Variance term	Estimate (SE)	Total variance (%)	p
Sections	σ^2_ε	0.349 (0.023)	34.9	
Reaches	$\sigma^2_{u_0}$	0.597 (0.096)	59.7	<0.001
Streams	$\sigma^2_{v_0}$	0.051 (0.060)	5.1	0.102

Note: HL (variance term): section (σ^2_ε), reach ($\sigma^2_{u_0}$), streams ($\sigma^2_{v_0}$). Variance among sections corresponds to the error term and has no associated p value. SE, standard error.

To account for serial correlation potentially arising between first-level residuals because of the proximity between sections within a reach, a first-order autoregressive (AR1) covariance structure with equal spatial intervals was included in the model:

$$\text{cov}(\varepsilon_{ij}, \varepsilon_{i-s,j}) = \sigma^2_\varepsilon e^{-\alpha s}$$

where s is the standardized distance between two sections in the same reach and α is a decay coefficient for the spatial autocorrelation, which is given by $e^{-\alpha s}$ (Yang et al. 2001; Hox 2002; Goldstein 2003). The section-level R^2 was obtained by squaring the Pearson correlation between observed values and values predicted by the full model.

Before analysis, brook trout density was transformed as $\ln(X + 1)$; environmental variables were transformed by use of logarithmic or power functions when necessary to reduce the influence of extreme points and better fit statistical assumptions of linearity, normality, and homoscedasticity. All variables were standardized to their grand mean to avoid nonessential colinearity between predictors and facilitate the interpretation of the intercept (Hox 2002).

Results

Brook trout were found in 89% of sections, 98% of reaches, and all streams. The decomposition of variance showed that variation in brook trout density among streams was small (5.2% of total variance) in relation to that among sections (35.3%) or reaches (59.5%) and not statistically significant (Table 2). The 21 potential predictors were not strongly intercorrelated: only 8 of 210 pairwise correlations were >0.5 in absolute value and all of the tolerances were

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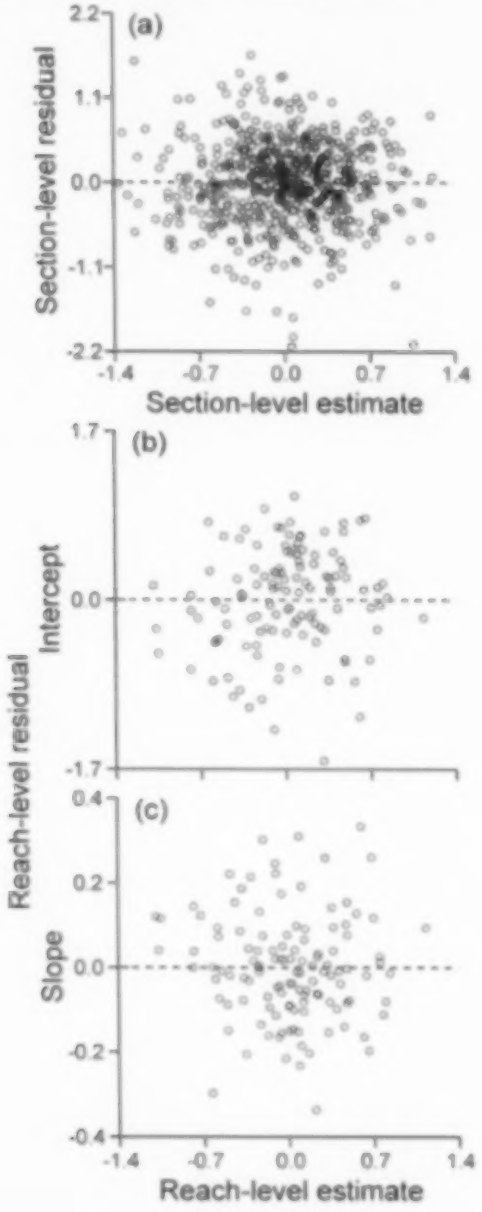
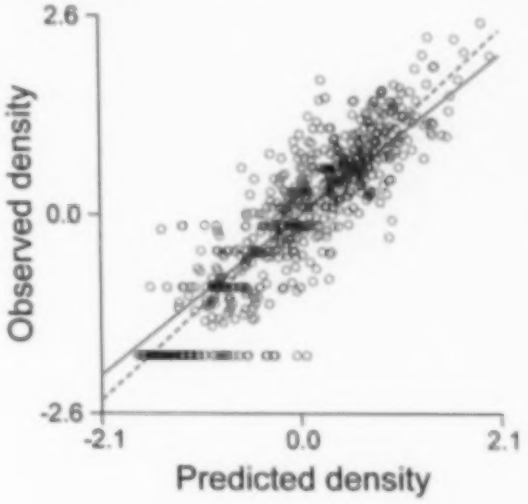
Fig. 2. Residual plots for section-level and reach-level residuals. (*a*) Section-level residuals are the differences between observed values and values predicted by reach-level regressions. (*b* and *c*) Reach-level residuals refer to the regression parameters for current velocity. (*b*) Reach-level residuals for the intercept are the differences between the estimated intercepts for each reach and the overall mean intercept. (*c*) Reach-level residuals for the slopes are the differences between the estimated slope for each reach and the overall mean slope. Residuals are plotted against the standardized density predicted by the fixed-effects part of the model.



≥0.06. The final regression model included three section-level predictors (current velocity, units of woody debris, and cover index), three reach-level predictors (subbasin area, valley width, and height increment at flood), and a cross-level interaction between current velocity and subbasin area. Although the spatial autocorrelation term was not statistically significant ($p = 0.075$), it was nevertheless kept in the model to adjust for the spatial relationship between sections. The tolerance for predictor variables in final models was always ≥0.75, indicating only mild colinearity among the predictors. Graphical analyses showed no apparent deviations from the assumptions of normality, homogeneity of variance (residual plots for the section and reach levels; Fig. 2), and linearity (scatterplot of observed vs. predicted values; Fig. 3).

Fig. 3. Scatterplot of observed vs. predicted densities of brook trout (*Salvelinus fontinalis*). Densities are standardized to zero mean and unit variance. Predicted values are from the full model including both fixed and random effects. One-to-one (solid) and regression (broken) lines are also shown. The horizontal row of values at the bottom of the figure represents sections where no fish were captured.



Brook trout density was positively related to woody debris and cover and negatively related to height increment at flood, valley width, and current velocity, but the relationship between brook trout density and current velocity varied markedly across reaches, as shown by the variation in the slope coefficients for current velocity (Fig. 4). This variation was related systematically to subbasin area, as revealed by the significant cross-level interaction between current velocity and subbasin area (Table 3). A graphical display of the cross-level interaction showed stronger decline with current velocity in larger subbasins than in smaller subbasins (Fig. 5).

Discussion

In the Cascapedia River basin, brook trout density did not vary significantly among streams, but varied substantially both among sections within reaches and among reaches. Although multiscale studies often examine the proportion of variation explained by environmental features at different

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Table 3. Coefficient estimates, standard errors, and p values for the fixed and random components of the hierarchical linear model.

Model term	Estimate	SE	p
Predictor variable (fixed coefficient)			
Intercept (β_0)	0.018	0.063	
Current velocity (β_1)	–0.221	0.044	<0.001
Large woody debris (β_2)	0.16	0.034	<0.001
Cover index (β_3)	0.103	0.042	<0.001
Subbasin area (β_4)	–0.164	0.069	0.008
Height increment at flood (β_5)	–0.226	0.07	<0.001
Valley width (β_6)	–0.129	0.068	0.003
Current velocity × subbasin area (β_7)	–0.093	0.043	0.032
Random components			
σ^2_ε	0.325	0.046	
$\sigma^2_{u_{0j}}$	0.36	0.066	<0.001
$\sigma^2_{u_{1j}}$	0.054	0.026	0.034
$\sigma_{u_{0j}u_{1j}}$	–0.05	0.028	0.034
Decay coefficient for spatial autocorrelation			
α	2.378[a]	0.521	0.075

Note: The coefficients for the intercept and current velocity have a fixed and a random part, i.e., $\beta_{0j} = \beta_0 + u_{0j}$, $\beta_{1j} = \beta_1 + u_{1j}$, with $u_{0j} \sim N(0,\sigma^2_{u_{0j}})$ and $u_{1j} \sim N(0,\sigma^2_{u_{1j}})$. The covariance between u_{0j} and u_{1j} is $\sigma_{u_{0j}u_{1j}}$. The autocorrelation decay coefficient is α. SE, standard error.

[a]Implies a spatial correlation of 0.186 between adjacent sections.

Fig. 4. Plot of predicted densities of brook trout (*Salvelinus fontinalis*) vs. current velocity at each of the 120 reaches. Densities and current velocity are standardized to zero mean and unit variance. Predicted values are from the model including both fixed and random effects for the intercept and current velocity.

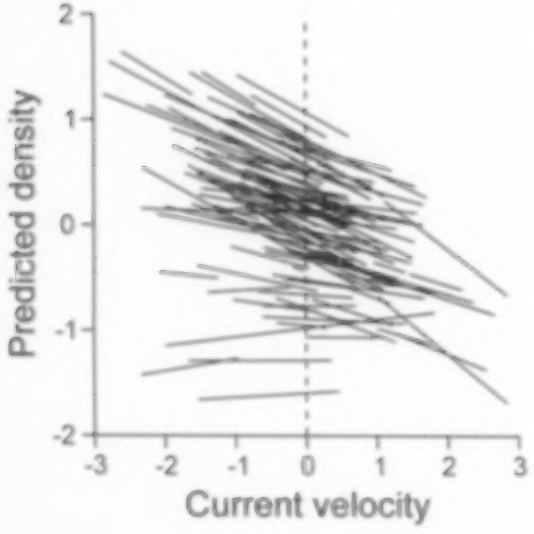
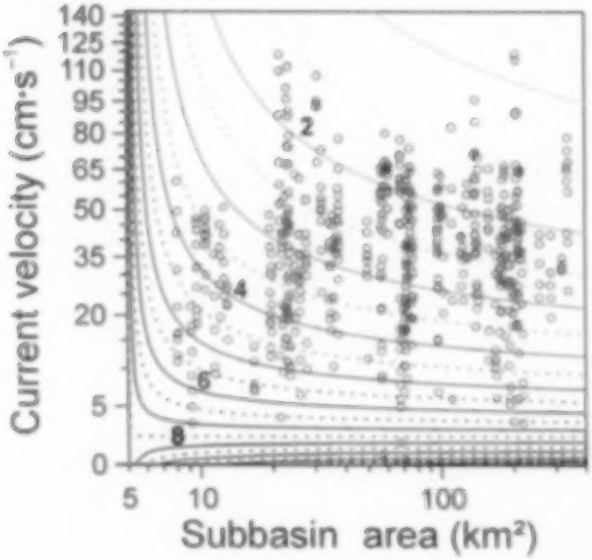


Fig. 5. Contour plot illustrating the effect of the cross-level interaction between current velocity, a section-level predictor, and subbasin area, a reach-level predictor, on density of brook trout (*Salvelinus fontinalis*). Contour lines represent density of brook trout (numbers·100 m^{-2}) as predicted by the fixed-effects part of the hierarchical linear model. The circles represent observed combinations of current velocity (cm·s^{-1}) and subbasin area (km^2) at individual sections; the dispersion of the circles reflects the joint variability in these two variables.



spatial scales (Milner et al. 1995; Watson and Hillman 1997), only a few of these studies have specifically quantified variation in fish abundance at each scale (e.g., Dunham and Vinyard 1997). Yet, the decomposition of variation in fish abundance can identify those scales at which populations vary most and can therefore guide the choice of environmental features and measurement grain needed in an analysis. In the present study, the results from the decomposition of variation motivated the use of a simplified

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hierarchical model focused on variation only at the section and reach scales.

The relationship between brook trout density and current velocity varied across reaches as a function of subbasin area. Brook trout density was weakly related to current velocity in reaches within smaller subbasins but declined markedly with current velocity in reaches within larger subbasins. This contextual effect may be linked to stream size, because subbasin area was positively related to stream width (Spearman rank correlation, $r_s = 0.85$) and stream order ($r_s = 0.63$), two measures of stream size. Velocity refugia are used by stream salmonids to maximise energy intake and minimise swimming costs (Grant and Noakes 1987; Fausch 1993; McLaughlin and Noakes 1998). Instream structures that create velocity refugia, such as boulders, provide energetically suitable locations for salmonids, resulting in greater population density (Fausch and Northcote 1992; McLaughlin and Noakes 1998). Structures such as boulders and woody debris tend to be less abundant in larger streams (Benke and Wallace 1990; Jowett et al. 1998; Wing and Skaugset 2002). Because of their greater depth, larger streams also have lower relative roughness, and thus smoother flow near the streambed, than smaller streams (Leopold et al. 1964). Water velocity may therefore have had greater influence on brook trout density in larger streams as a result of the lower availability of velocity refugia in those streams.

Within reaches, brook trout density was greater in sections with more woody debris and cover. Large woody debris and cover are thought to enhance the habitat suitability of streams for salmonids by providing low-velocity refugia during floods, profitable feeding positions of low velocity next to high-velocity patches, and visual isolation that reduces interference competition and risk of predation (McMahon and Hartman 1989; Fausch 1993; Inoue et al. 1997). Woody debris acts as additional substratum for macroinvertebrates, usually resulting in higher food abundance for fish (Dolloff 1986; Harmon et al. 1986). Large woody debris is also associated with the development of pools (Andrus et al. 1988; Carlson et al. 1990), a preferred habitat for brook trout (Gibson et al. 1993; Rodríguez 1995; Bélanger and Rodríguez 2002).

Brook trout density was negatively related to height increment at flood and valley width. Negative effects of high flows on stream fish abundance are well documented (Freeman et al. 2001; Roghair et al. 2002; Lobón-Cerviá and Rincón 2004). High flows may increase egg and yearling mortality or displace juvenile and older fish (Erman et al. 1988; McMahon and Hartman 1989; Carline and McCullough 2003). Brook trout displaced experimentally in a natural stream tended to settle in preferred habitats away from their home site (Bélanger and Rodríguez 2001); in the absence of effective homing, population density may remain low for extended periods in stream reaches where brook trout are displaced by high flow events. The negative relation between brook trout density and valley width may be mediated by geomorphic processes related to longitudinal variation. Valley width was related negatively to entrenchment ($r_s = -0.57$) and stream gradient ($r_s = -0.38$). Other studies have found greater fish density (Rabeni and Sowa 1996) or better spawning substratum (Coulombe-Pontbriand and Lapointe 2004) in narrower, more entrenched, upstream segments than in wider downstream segments, which have shallower slopes, a greater proportion of gravel and sand, and a smaller proportion of cobbles and boulder in the streambed (Rabeni and Sowa 1996; Isaak and Hubert 2000). This result suggests that large-scale fluvial dynamics contributed to determining brook trout density at the reach scale.

Hierarchical models account for the intragroup correlation inherent to nested sampling designs and can therefore properly assess the statistical significance of potential predictors, hence improving the reliability of these models relative to conventional approaches such as multiple regression based on ordinary least squares. In many studies, the problem of intragroup correlation has been dealt with by aggregating observations at the higher levels and working with group means, examining small-scale (lower-level) patterns separately for each higher-level group, or a combination of both (e.g., Inoue et al. 1997; Watson and Hillman 1997; Angermeier and Winston 1999). However, these approaches usually leave among-group differences in small-scale patterns unexamined and can also lead to loss of information and statistical power (Hox 2002; Goldstein 2003).

Although hierarchical models are often used in aquatic ecology to account for spatial or temporal correlation between sampling units, their potential to enhance our understanding of patterns of species distribution at multiple spatial scales still remains largely untapped. The relationships between brook trout density and individual environmental features in this study are broadly in agreement with findings from previous studies; however, the hierarchical modelling approach additionally allowed for detection and proper statistical treatment of the effect of reach-level variables and the contextual effect of section-level variables on brook trout density. By accounting for the nested sampling design and simultaneously using the information available at all spatial scales, the hierarchical model allowed us to detect a cross-level interaction between environmental predictors at the section and reach levels that by definition would not have been detectable had we aggregated the data by averaging observations from individual sections. The presence of a cross-level interaction illustrates that patterns uncovered at smaller scales cannot always be extrapolated to larger scales and supports the notion that there is no single "best scale" at which to examine the relationships between fish distribution or abundance and environmental features (Schneider 2001).

Acknowledgements

We thank V. Bérard, K. Brassard, C. Cossette, M.-J. Gagnon, E. Racicot, and C. Sauvé for expert field assistance, M.-A. Bernard, M. Gauthier, and la Société de la faune et des parcs du Québec for logistic support, and M. Lapointe for advice on site selection. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada, le Fonds Québécois de la recherche sur la nature et les technologies, la Société Cascapédia, le Centre interuniversitaire de recherche sur le saumon atlantique (CIRSA), and le Syndicat des professeurs et professeures de l'UQTR. This paper is a contribution to the CIRSA program.

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Carry-over effects in brown trout (*Salmo trutta*): hypoxia on embryos impairs predator avoidance by alevins in experimental channels

Jean-Marc Roussel

Abstract: Laboratory experiments on brown trout (*Salmo trutta*) embryos suggest that sublethal stress in the gravel nest such as hypoxia may alter the behaviour and survival of fish during the early juvenile period. Eggs and embryos were incubated at constant temperature (8.2 °C ± 0.6 standard deviation) under nonlethal dissolved oxygen (DO) concentrations (3.0 mg·L^{-1}; 26% air saturation level) and normoxia (10.3 mg·L^{-1} DO; 90% air saturation level). The average survival from fertilization to end of embryonic development was 70% and 85% for hypoxic and normoxic groups, respectively. Hypoxic embryos grew slowly compared with their normoxic counterparts, but similar body sizes were observed when yolk-sac absorption was completed. Fish incubated as hypoxic embryos delayed their emergence from the gravel in experimental channels. In presence of freshwater sculpin (*Cottus gobio*), their swimming activity was reduced by 20%, on average, and predation was enhanced by 14% compared with normoxic groups. Results support the view that subtle events early in a fish's ontogeny can have carry-over effects on later periods of its life cycle, and this phenomenon may be a significant source of variation in salmonid fitness.

Résumé : Des expériences en laboratoire sur la truite brune (*Salmo trutta*) indiquent qu'un stress sublétal, tel qu'une hypoxie, dans les nids de gravier, peut altérer le comportement et affecter la survie des poissons au début de leur période juvénile. Des oeufs et des embryons incubés à température constante (8,2 °C ± 0,6, écart type) à des concentrations non létales d'oxygène dissous (OD 3,0 mg·L^{-1}, 26 % de saturation avec l'air) et en normoxie (OD 10,3 mg·L^{-1}, saturation avec l'air) ont des survies moyennes respectives de 70 % (hypoxie) et de 85 % (normoxie), de la fécondation à la fin du développement embryonnaire. Les embryons hypoxiques croissent plus lentement que leurs semblables normoxiques, mais ils atteignent des tailles comparables au moment de la fin de la résorption du sac vitellin. Dans des canaux expérimentaux, les poissons incubés en hypoxie durant l'embryogenèse retardent leur émergence du gravier. En présence de chabots (*Cottus gobio*), leur activité de nage est réduite en moyenne de 20 % et leur prédation accrue de 14 % par comparaison aux groupes normoxiques. Ces résultats appuient l'idée que des événements de faible importance durant le début de l'ontogénie d'un poisson peuvent avoir des effets à long terme durant les périodes subséquentes du cycle biologique et que ce phénomène peut être une source significative de variation de la fitness chez les salmonidés.

[Traduit par la Rédaction]

Introduction

Species with complex life cycles are prone to high temporal variations in mortality rate during their life history, which are closely related to transitions between life periods (sensu Balon 1975). The ontogenetic habitat transition between the larval and juvenile periods is a critical time that involves rapid changes in behaviour as organisms are adapting to new surroundings and lifestyles. Consequently, high mortality rates have been reported during the early juvenile period of many aquatic species, including invertebrates (Gosselin and Qian 1997; Hunt and Scheibling 1997), amphibians (Smith 1983; Berven 1990), and fish (Doherty and Sale 1986; Webster 2002). However, most studies focus on direct mortality causes, with no or little information on embryonic and larval history. That this issue may be of concern is suggested by the increasing evidence that conditions experienced during early life may have negative effects on later life fitness. These carry-over effects between a juvenile's performance and larval or embryonic experience have already been described in bryozoans (Wendt 1998), gastropods (Pechenik et al. 1998), bivalve molluscs (Phillips 2002), insects (Taylor et al. 1998), amphibians (Pahkala et al. 2001), and fish (Searcy and Sponaugle 2001). For fish, environmental conditions experienced by pelagic larvae of marine species can affect juvenile growth and vulnerability to predators during the early posttransition period (McCormick and Hoey 2004; Phillips 2004). But surprisingly, little attention has been paid to the existence of such carry-over effects in freshwater fish.

Of particular interest is the case of salmonid species that hide their brood in substrates (lithophile sensu Balon 1981). A remarkable ontogenetic habitat transition occurs at the be-

Received 20 July 2006. Accepted 2 March 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 12 June 2007. J19434

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 doi:10.1139/F07-055 © 2007 NRC Canada

ginning of the alevin phase (defined as the first phase of the juvenile period; Balon 1975), when alevins emerge from the gravel into the open water, start exogenous feeding, and are confronted with predaceous species. Because postemergent individuals rapidly gain experience, it is reasonable to suppose that emergence is the time of greatest risk during the early juvenile period. Embryonic development in salmonids depends on the interaction of several environmental factors, including water temperature (Ojanguren and Brana 2003), intragravel water quality (Malcolm et al. 2003), substratum permeability (Rubin and Glimsater 1996), and the presence of fine sediments in the redd environment (Olsson and Persson 1988). In particular, the detrimental effects of low dissolved oxygen (DO) levels on developing embryos have been investigated, primarily focussing on embryo mortality, size, and deformity and premature or protracted hatching and emergence (e.g., Winnicki 1967; Sowden and Power 1985; Latham and Just 1989). The present study explores the hypothesis that long-term hypoxia on embryos could modify the subsequent fitness of brown trout (*Salmo trutta*) during the early juvenile period. We focus on variables that are likely to affect individual fitness and recruitment, such as embryonic survival, growth, developmental anomalies, dates of emergence, and swimming capacity of recently emerged juveniles and their vulnerability to predators.

Materials and methods

Incubation of brown trout embryos

The study was conducted over two consecutive years, 2001 and 2002. Eggs were obtained by manual stripping of three (2001) and five (2002) female brown trout (fork length 220–305 mm) caught in the River Oir (Normandy, France). After fertilization, the eight batches (labelled from A to H) were divided into two groups and settled in incubators supplied with circulated water. Number of eggs varied from 370 to 1090 depending on the batch. Incubators were vertical cylinders (20 cm × 20 cm) with a plastic tray on which the eggs were laid out. For each batch, there was one incubator with normal oxygen supply (referred to as normoxic), and one incubator supplied with water at a lower and constant O_2 level (referred to as hypoxic). Normoxic water came from a tank equipped with an aeration system (air bubbling), whereas hypoxic water was obtained by using an oxygen-depletion system adapted from Miller (1992). DO was removed by injection of atmospheric nitrogen (N_2) into a vertical column into which the water was flowing. The oxygen depletion was controlled by the flow of N_2 coming from a tank equipped with a regulator. Surface gas exchange in incubators was limited by setting covers (plastic plates) on the water surface. During incubation, the oxygen levels were checked manually twice a day using an oxymeter (WTW oxy 320 and oxygen electrode Cellox 325, Wissenschaftlich Technische Werkstätten GmbH, Germany) and were adjusted when necessary. The average DO concentration was 10.3 mg·L^{-1} (±0.4 standard deviation (SD), 90% air saturation level) for normoxic incubators and 3.0 mg·L^{-1} (±0.5 SD, 26% air saturation level) for hypoxic incubators. Air conditioning maintained a constant temperature in the incubation room; water temperature was automatically recorded every hour (Vemco Minilog 8-bit datalogger, Shad Bay, Nova Scotia) and averaged 8.2 °C (±0.6 SD) during the experiment.

Mortality was checked daily, and dead eggs and embryos were removed to prevent parasite and fungus infection. Individuals were classified as anomalous if they had flexure of the spinal column. In 2001, we carried out a more detailed investigation of the effect of hypoxia on vertebrae numbers and vertebral column defects. We randomly selected hypoxic and normoxic embryos in each incubator before complete yolk adsorption and then reared them in two circular tanks supplied with recirculating water. Fish were fed during daytime with commercial food pellets over a period of 8 weeks, i.e., until they reached a sufficient size (5–7 cm fork length) for X-ray analysis. Thirty fish were selected at random in each tank and were overanaesthetized in a solution of phenoxy-ethanol (0.1%), and X-ray photographs were taken using a medical Phasix 65 camera (CGR Koch and Sterzel, Germany) and Kodak X-O.MAT MA film.

In 2002, the growth of embryos was monitored from hatching to complete yolk absorption. Every 7 days, embryos (n = 11) were randomly sampled from each incubator (five batches, hypoxic and normoxic groups), individually photographed using a digital camera (Sony DCR-TRV 110E, Sony, Japan), and then returned to the incubators. No anaesthetic was used. Photographs were processed with Adobe Photoshop Pro 6.0, where the length of the embryos was measured from nose to caudal fin to the nearest 0.2 mm. The fork length was measured when the posterior margin of the caudal fin changed from being convex to slightly concave (developing fork). The end of embryonic development was determined according to the criteria of Killeen et al. (1999).

Emergence and predator–prey experiments

Predator–prey experiments were conducted in four indoor channels (5 m long × 0.48 m wide × 0.25 m high) made of fibre glass and reinforced polyester, with an adjustable overflow at the end of the channels. Removable partitions consisting of plastic frames supporting a stainless-steel mesh (1 mm) were placed 50 cm downstream from the inlet and 50 cm upstream from the outlet to hinder movement of fish out of the channels. A hole (60 mm diameter) in the partitions was connected to a trap to catch alevins moving upstream or downstream after emergence. Previous investigations in similar experimental channels have indicated that brown trout alevins emigrate immediately upon emergence (Roussel and Bardonnet 1999; Bardonnet et al. 2006). A screen across the holes (1 cm mesh) prevented predators from entering the traps. The outflowing water was fed into an 800 L reservoir and pumped to the upstream end of the channels. During the experiment, the recirculating water was well oxygenated (90%–100% oxygen saturation) and kept at constant temperature (12.1 °C ± 0.3 SD). The channels were enclosed by wooden walls with a narrow window on one side (4 cm high) to allow observations. Mirrors were placed above the channels to provide a full cross-sectional view to the operator standing in front of the window. Illumination came from neon tubes (Mazdafluor, Daylight 365), beginning at 0730 and lasting for 11.5 h. Twice a day, from 0700 to 0730 and from 1900 to 1930, dawn and dusk were simulated by 30 min of gradually changing illumination. The

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channels were filled with a 5 to 6 cm gravel bed (10–35 mm particle diameter) set above a bottom at two different heights across the channel to create a 12 cm deep habitat with a 2 cm deep margin. Based on 20 evenly spaced point measurements per channel, the velocity at 0.4 of the water depth ranged from 10 to 13 cm·s^{-1} in the deep habitats and from 0 to 12 cm·s^{-1} at the margins; water velocities in the channels were mostly less than the critical velocity for emerging brown trout (Heggenes and Traaen 1988).

Seventy-five days after fertilization (corresponding to step 37 R3 in the study of Killeen et al. (1999)), embryos from batches B, D, and G were randomly selected and transferred to channels. The same procedure was followed for each batch: after progressive acclimatization to water temperature, 60 embryos per channel were placed 60 cm apart in groups of 10 under the gravel in the deep habitat. For each batch, two channels were stocked with normoxic embryos and two channels were stocked with hypoxic embryos. Control groups of 20 embryos of each batch were also placed into incubators and positioned between the downstream partition and the outlet in each channel to monitor mortality throughout the experimental period. Alevin traps were checked every day at 0800 (after dawn) to monitor the time dynamics of postemergence displacements, and daily observations of fish behaviour were carried out at 1000, 1300, and 1600. The operator moved discretely along to the upstream end of the channel to look for emerged young trout. When a fish was encountered, its posture was classified as either (*i*) immobile (fish lying on the substrate) or (*ii*) swimming (fish maintaining position against the current or alternating between swimming and bottom contact). Occasionally, fish moved from one position in the channel to another during the observation and were classified as swimming. Approximately 10 min were necessary to perform observations in one channel.

One week before the expected date of emergence, predators (freshwater sculpin, *Cottus gobio*) were electrofished in the Oir River. Males of similar size (total length range 6.8–7.6 cm) were chosen and immediately transferred to the laboratory. They were placed individually in cages consisting of plastic frames (20 cm) supporting plastic mesh (1 mm) and put into a tank supplied with well-oxygenated water (air bubbling system) at constant temperature (12 °C). The time in cage (between capture and transfer to channels) varied from 6 to 8 days. During this period, one live brown trout embryo was introduced into each cage in the morning to feed the sculpin. If the predator did not eat its prey, it was automatically excluded from the experiment. This procedure ensured that all predators had a similar daily feeding ration until their introduction into the channels. Dates of transfer to the channels were determined as follows: a minimum of three individuals (5% of the stock) were visible in the channel and at least one alevin was trapped in the morning. Three sculpin were released into each channel at 1700 for a period of 10 days. This period corresponds to the duration of emergence and postemergence displacement as previously observed in similar channels and experimental settling conditions (Roussel and Bardonnet 1999). At the end of the 10-day period, the gravel bed was completely removed from each channel, and surviving juveniles were collected.

Data analysis

No mortality was recorded in the control incubators that were placed in each channel, so the proportion of juveniles eaten (P_n) was estimated as

$$P_n = (60 - S_n - T_n)/60$$

where S_n is the number of survivors in channel n and T_n is the cumulative number of juveniles caught in traps of channel n during the 10-day period. At the end of the experiments, all surviving fish were overanaesthetized in a solution of phenoxy-ethanol (0.1%).

The growth of embryos was computed using the von Bertalanffy model:

$$l_t = L_\infty[1 - e^{-K(t-t_0)}]$$

where l_t is the length of embryo at time t, L_∞ defines an asymptotic or maximum body length, K is the growth coefficient (defining growth rate toward the maximum), and t_0 is the age at which the embryo would have length zero assuming this growth model applies at all ages.

Student's t tests were used to test differences between normoxic and hypoxic groups (number of vertebrae, incubation length, size of embryos, swimming activity, and predation). When heteroscedasticity or deviation from normality was detected, nonparametric Wilcoxon–Mann–Whitney rank sum tests were used. Statistical significance was set at $\alpha = 0.05$.

Results

Mortality of embryos and developmental anomalies

The proportion of embryos that died in incubators varied from 0.01 to 0.80 depending on the batch. Survival until absorption of the yolk sac was lower, on average, under hypoxia (70%) compared with normoxia (85%). However, it is noteworthy that exposure to low DO level had an effect on only three of the eight batches (B, C, and E) for which mortality was 11%–35% higher compared with normoxic embryos (Fig. 1). Whatever the treatment (hypoxia or normoxia), 95% of mortality occurred before hatching. The proportion of developmental anomalies at hatching was less then 1%, whatever the batch or treatment. X-ray photographs did not reveal skeleton anomalies, such as the presence of malformed or fused vertebral bodies, for juveniles that had been exposed to hypoxia as embryos. The mean (±SD) number of vertebrae did not vary between the treatments (hypoxia, 60.4 ± 0.8; normoxia 60.0 ± 1.1; Wilcoxon–Mann–Whitney test, $Z = 1.539$, $p = 0.124$).

Growth of embryos

Hatching started 57–58 days after fertilization, whatever the treatment. However, time from the hatching of the first to the last egg was longer in hypoxic (5–10 days) than in normoxic groups (2–4 days) (Wilcoxon–Mann–Whitney test, $Z = -3.381$, $p = 0.0007$). At hatching (Fig. 2), hypoxic embryos were smaller (mean body length 14.0 mm ± 0.7 SD) than normoxic embryos (16.8 mm ± 0.7 SD) (t test, df = 108, $t = -21.142$, $p = 0.0001$). Time until the end of development (step 40 R6, Killeen et al. (1999)) was affected by low DO level during incubation (Wilcoxon–Mann–Whitney

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Fig. 1. Mortality of brown trout (*Salmo trutta*) from fertilization to end of embryonic development, given as the proportion of embryos that died when incubated under normoxia (*x* axis) or hypoxia (*y* axis). The different batches are labelled from A to H; the $y = x$ line is displayed.

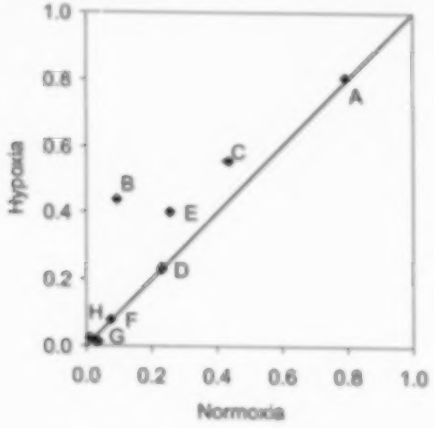
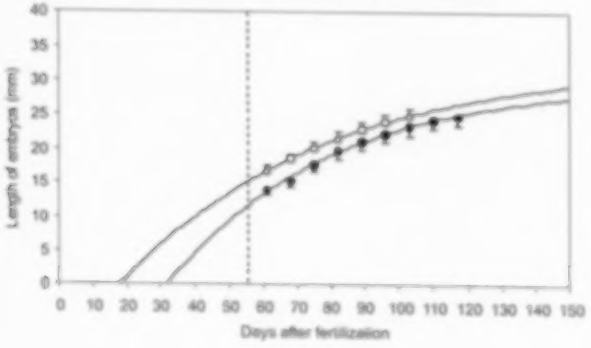


Fig. 2. Embryonic growth in brown trout (*Salmo trutta*), from hatching to complete yolk absorption, when incubated at 8.2 °C (±0.6 standard deviation) under normoxia (○) or hypoxia (●). Results are given as mean, vertical lines represent standard deviations, with von Bertalanffy growth models plotted as solid curves. Broken line indicates the beginning of hatching.



test, $Z = -3.313$, $p = 0.0009$). Depending on the batch, the embryonic development ended 88–97 days after fertilization in normoxic groups, whereas hypoxic embryos completed their development 100–110 days after fertilization.

On completion of yolk absorption, no difference in size was detected between normoxic embryos (mean fork length 24.8 mm ± 1.1 SD, measured 103 days after fertilization) and hypoxic embryos (24.8 mm ± 1.3 SD, measured 117 days after fertilization) (*t* test, df = 108, $t = -0.2757$, $p = 0.7833$). Von Bertalanffy growth model curves fitted to embryo length measurements indicated that the asymptotic body length l_∞ of normoxic groups was more than that of hypoxic groups (32.9 mm ± 2.0 standard error (SE) vs. 30.1 mm ± 0.9 SE, respectively); the growth coefficient K was higher for hypoxic embryos (0.0209 ± 0.0019 SE) than for normoxic embryos (0.0166 ± 0.0029 SE).

Fig. 3. Emergence time (in days after fertilization) given as number of *Salmo trutta* alevins trapped in each channel, for alevins incubated as normoxic embryos (○ and solid lines) or hypoxic embryos (● and broken lines). Bold lines represent average profiles of emergence for each treatment. Vertical broken line indicates the date at which embryos were transferred into channels.

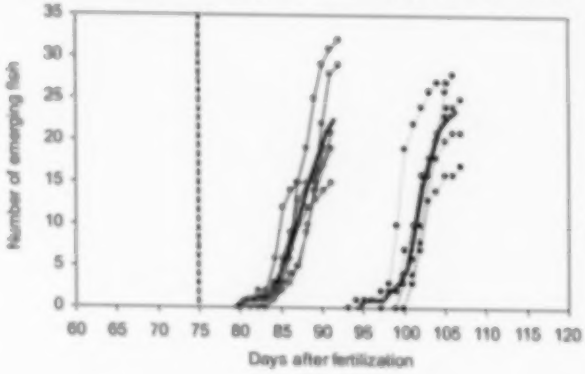
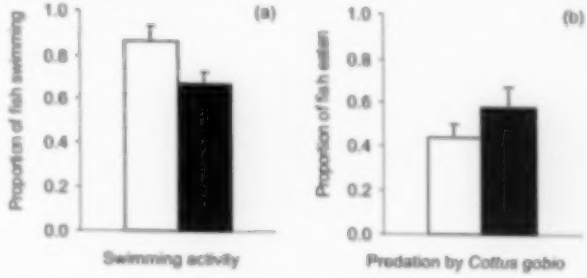


Fig. 4. (*a*) Mean (± standard deviation (SD)) proportion of alevins that swim in the water column, and (*b*) mean (± SD) number of alevins eaten by the sculpin *Cottus gobio* in experimental channels, after being exposed to hypoxia (solid bars) or normoxia (open bars) as embryos.



Emergence, behaviour, and predation

After transfer to experimental channels, hypoxic embryos delayed their emergence from the gravel compared with normoxic embryos (Fig. 3). First-emerging fish were trapped 81–84 days after fertilization in channels that had been stocked with normoxic embryos, whereas fish from hypoxic groups started to emerge and leave the channels 94–101 days after fertilization. The average profiles of emergence were then similar whatever the treatment. Over the period of emergence, the average number of alevins observed were 5.6 (±2.9 SD) and 10.1 (±6.9 SD) in channels stocked with hypoxic and normoxic embryos, respectively.

The average proportion of juveniles remaining immobile on the bottom was significantly higher in hypoxic groups (0.33 ± 0.05 SD) than in normoxic groups (0.13 ± 0.06 SD) (Wilcoxon–Mann–Whitney test, $Z = -2.8072$, $p = 0.0050$; Fig. 4*a*). Significantly more juveniles were eaten by the sculpin *Cottus gobio* in channels stocked with hypoxic embryos (34.7 ± 5.7 SD) vs. normoxic embryos (26.5 ± 3.6 SD) during the period of emergence (Wilcoxon–Mann–Whitney, $Z = 2.1655$, $p = 0.030$;

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Fig. 4*b*). For all batches combined, sculpin preyed on 10%–19% more hypoxic embryos than normoxic embryos.

Discussion

The critical DO values that affect survival of salmonids to hatching range between 5 mg·L^{-1} and 11 mg·L^{-1} depending on species and river (e.g., Curry et al. 1995; Ingendahl 2001; Malcolm et al. 2003). The causal link between DO and embryo survival has been established under experimental conditions (e.g., Alderdice et al. 1958; Silver et al. 1963; Shumway et al. 1964), but lower critical DO values (1–8 mg·L^{-1}) suggest the existence of some correlated variables affecting survival in the wild. The present study shows that low DO levels (3 mg·L^{-1}) have some deleterious effects on the survival of brown trout embryo (–15% on average). More than 95% of embryo mortality induced by hypoxia occurs before hatching, but survival was affected in only three out of eight batches. The egg capsule, including the perivitelline fluid, represents an oxygen barrier, as shown by the fall in oxygen tension at which O_2 becomes limiting on removal of the egg capsule or when hatching (Rombough 1986; Czerkies et al. 2002). There are considerable variations in the egg capsule structure and oxygen conductance among salmonids and between individuals of the same species (Groot and Alderdice 1985; Rombough 1989), and more work is needed to clarify the sources of such individual variations and to understand the ability of eggs to survive hypoxic stress in redds.

In addition to direct mortality, low oxygen concentrations in redds have sublethal effects on embryos by modifying the body growth and the time frame of ontogenetic development. In this experiment, a low DO level slightly prolongs hatching but dramatically reduces (by 17%, on average) the size of recently hatched embryos. Interestingly, hypoxia has a slightly positive effect on embryonic growth during the posthatching period, suggesting that compensatory growth may occur for free embryos even under hypoxic conditions (3 mg DO·L^{-1}). Oxygen requirements of salmonid embryos usually rise to a maximum just before hatching (Alderdice et al. 1958; Hamor and Garside 1977; Rombough 1986). Matschak et al. (1997, 1998) pointed out the deleterious effect of the vitelline envelope on gas exchange processes and the sensitivity of embryos to oxygen shortage. They measured fibre numbers and enzymatic activities in muscle tissue of Atlantic salmon (*Salmo salar*) embryos subjected to conditions of low DO levels (50% air saturation level). They found a reduction in metabolism and growth except when the egg capsules were removed. Along the same line of research, Czerkies et al. (2002) observed a decrease in heart rate (bradycardia) for embryos of two coregonid species (*Salmonidae*) exposed to hypoxia and reported that bradycardia was lower after removing the egg capsule. Accordingly, the deficit in growth before hatching suggests a reduction in oxygen transfer to the embryo, thus reinforcing the hypothesis that the egg capsule has an unfavourable effect on gas exchange.

In spite of a slightly higher growth rate during the posthatching period, hypoxic embryos achieve yolk adsorption later than normoxic embryos. However, no difference in body length is observed when the yolk is digested. Literature on the fate of hypoxic embryos confirms that complete adsorption of the yolk is generally delayed (Winnicki 1967; Chapman 1988; Massa et al. 1999). For many species, significant differences in the body length and weight of hatching embryos had been reported when yolk is digested (*Oncorhynchus kisutch*, Mason 1969; *Salmo salar*, Hamor and Garside 1977; *Salmo trutta*, Massa et al. 1999), at emergence (*Oncorhynchus mykiss*, Miller 1988) or at first feeding (*Salvelinus namaycush*, Carlson and Siefert 1974). After being exposed to long hypoxic episodes, brown trout embryos delay their emergence from the gravel when transferred to normoxic conditions in experimental channels. In the period following this transfer, embryonic development is completed, and at emergence, juveniles from the hypoxic groups are neither premature nor smaller than those from the normoxic groups. In the wild, some authors have observed that posthatch embryos can move within the substrate (Garcia de Leaniz et al. 1993). This suggests that the hatched embryos can avoid unsuitable microhabitats that provide insufficient DO because of low substrate permeability or the presence of fine sediments in the redds. Therefore, the presence of yolk embryos in streams probably indicates poor substrate quality, so that embryos are unable to find any normoxic microhabitats within the gravel and may be forced to emerge prematurely.

Going beyond the direct impact on embryos, recent studies on aquatic species from a wide range of taxonomic groups indicate that a juvenile's capacity to survive and grow can be related to conditions experienced early in its ontogeny. For instance, exposure of eggs and larvae to predators, competitors, or abiotic stressors can affect morphology, behaviour, growth, and survival of pre- and post-metamorphic amphibians (European frog (*Rana temporaria*), Pahkala et al. 2001; gray treefrog (*Hyla versicolor*), Relyea and Hoverman 2003; striped marsh frog (*Limnodynastes peronii*), Broomhall 2004). Similarly, various studies have stressed the importance of swimming duration and feeding history of marine larvae on survival and growth of juveniles and adults (bryozoan *Bugula neritina*, Wendt 1998; marine mussel *Mytilus galloprovincialis*, Phillips 2004; prosobranch gastropod *Crepidula fornicate*, Pechenik et al. 2002; barnacle *Balanus amphitrite*, Pechenik et al. 1998). Other recent studies on coral reef fishes have shown that high larval growth rate leads to an enhancement of postsettlement survival and growth of juveniles (Searcy and Sponaugle 2001; McCormick and Hoey 2004). In spite of this growing body of evidence, few studies to date have attempted to elucidate how traits are linked developmentally through ontogeny in freshwater fish literature. Mason (1969) observed that *Oncorhynchus kisutch* juveniles reared in tanks were smaller at emergence when they had been incubated under hypoxia and were more susceptible to emigrate when competing for food and space with normoxic juveniles. However, water temperature was increased in Mason's study to compensate for the delay in development resulting from lowered oxygen concentrations. Recent investigations on brown trout by Ojanguren and Brana (2003) have shown that the size of embryos at the time of first feeding decreases with increasing water temperature, and this factor could have affected the results and conclusions of Mason's study.

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In the present study, incubations were carried out at constant water temperature, and alevins exposed to hypoxia as embryos were no smaller than alevins from normoxic embryos. No evidence of morphological anomalies or vertebrae deformities was found, but juveniles from hypoxic groups underwent higher mortality by predation in the experimental channels. The proportion of alevins swimming in the water column was higher in the normoxic groups than in the hypoxic groups, suggesting that swimming ability was altered in fish from the hypoxic groups. Locomotor activity, particularly high-acceleration swimming behaviour, is important for escaping from predators during the early juvenile period of salmonid fishes. The high-acceleration performance in brown trout reaches its maximum at the end of yolk-sac absorption, i.e., when fish emerge from redds and become juveniles (Hale 1999). Because low-oxygen conditions during embryogenesis are known to affect muscle development (Matschak et al. 1997, 1998), it is likely that juveniles exposed to low DO levels as embryos suffer a reduction in their swimming capabilities mediated by changes in muscle phenotype, although this remains to be tested. Such a deficiency would lead to lower escaping performance and higher vulnerability when alevins leave the well-protected gravel nest and first confront predaceous species such as the sculpin *Cottus gobio*.

In conclusion, it is widely known that salmonid stocks decline when land use increases sedimentation in streams (Reeves et al. 1993; Waters 1995). Intensive use of land for agricultural and forestry practices has increasingly modified hydrological pathways and sediment transport in streams. The deposition of fine sediment in gravel bedded rivers and the retention of particles in hyporheic pore spaces alter the filtration at depth and water quality in streambeds (Boulton et al. 1998; Brunke 1999). Low DO concentrations directly impair the survival of salmonid embryos in redds (Ingendahl 2001; Malcolm et al. 2003) and lead to delays in the emergence of juveniles from the nest, as observed in the present experiment. Timing of emergence is a prime factor influencing offspring success, and some authors have demonstrated selection against late-emergent juveniles (Einum and Fleming 2000). Moreover, hypoxic conditions in redds modify fish behaviour and vulnerability to predators during the early posttransition time, when juveniles settle into their new open-water environment. We now require further investigations to quantify to what extent redd environments can account for the wide intraspecific variations of phenotypic traits and individual performances observed in juvenile salmonid populations.

Acknowledgements

The following persons and agencies are gratefully acknowledged: D. Azam, J.-M. Le Quere, P.-M. Lucas, and J. Tremblay for design and maintenance of the oxygen depletion system; D. Huteau for dissolved oxygen measurements and analysis of embryo length photographs; J. Aubin and A. Kacem for analysis of X-ray photographs; A. Quemener for construction and maintenance of the indoor channels; and F. Marchand and R. Delanoë (Conseil Supérieur de la Pêche) for field assistance. R.A. Cunjak and D. Morris made helpful comments on the draft, and M.S.N. Carpenter postedited the English style. Funding was provided by the "AIP AQUAE" programme from INRA and CEMAGREF.

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Overwintering of sea trout (*Salmo trutta*) in freshwater: escaping salt and low temperature or an alternate life strategy?

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Abstract: Brown trout (*Salmo trutta*) show large phenotypic plasticity. Juveniles may reside in their native freshwater habitat until maturation or migrate into the ocean as 1- to 3-year-old smolts. Sea-going fish (sea trout) reside at sea for 2–3 years until migrating back to their native stream for reproduction. However, immature fish may leave the ocean during their first or second winter at sea and overwinter in freshwater. The question is why does this occur? We tested the hypothesis that hypo-osmoregulatory capacity is compromised by low temperature in two coastal sea trout populations, one representing high salinity and the other, low salinity. Immature sea-run trout were caught in lower parts of two rivers during winter and acclimated to laboratory conditions. Subgroups were challenged with high salinity or low water temperature or both, and their osmoregulatory performance was investigated. Low temperature compromised the hypo-osmoregulatory ability, as indicated by insufficient compensatory adjustments of ion-transport mechanisms. Tagging experiments revealed that descent of overwintering fish into the ocean occurred over a narrow time period coincident with increasing water temperature. We conclude that overwintering in freshwater is partly driven by compromised osmoregulatory physiology, but because not all fish in a population do so, the phenomenon may also reflect diverging life strategies.

Résumé : La truite brune (*Salmo trutta*) affiche une importante plasticité phénotypique. Les jeunes peuvent demeurer dans les eaux douces où ils sont nés jusqu'à leur maturation ou alors ils peuvent migrer vers l'océan comme saumoneaux à l'âge de 1–3 ans. Les poissons qui vont en mer (truites de mer) y demeurent 2–3 ans avant de retourner dans le cours d'eau de leur naissance pour s'y reproduire. Cependant, les poissons immatures peuvent quitter l'océan durant leur premier ou deuxième hiver en mer pour passer l'hiver en l'eau douce. La question est de savoir pourquoi cela se passe ainsi. Nous testons l'hypothèse selon laquelle la capacité d'hypo-osmorégulation est affaiblie par les températures basses chez la truite de mer, représentée par deux populations, une population côtière de forte salinité et une autre de basse salinité. Nous avons récolté des truites de mer immatures en migration vers l'océan dans le cours inférieur de deux rivières durant l'hiver et les avons acclimatées aux conditions de laboratoire. Des sous-groupes ont été confrontés à une salinité élevée, une température basse ou les deux et leur performance d'osmorégulation a été déterminée. Une température basse diminue la capacité d'hypo-osmorégulation, comme l'indiquent les ajustements compensatoires insuffisants des mécanismes de transport d'ions. Des expériences de marquage indiquent que la descente vers l'océan des poissons durant l'hiver se produit durant une courte période de temps qui coïncide avec une augmentation des températures de l'eau. Nous concluons que le passage de l'hiver en l'eau douce est en partie contrôlé par une physiologie de l'osmorégulation affaiblie; cependant, comme tous les poissons dans la population n'agissent pas ainsi, le phénomène peut aussi refléter des stratégies biologiques différentes.

[Traduit par la Rédaction]

Introduction

The brown trout (*Salmo trutta*) is a salmonid species with great diversity in morphology and life history pattern (L'Abée-Lund et al. 1989). Stream, lake, and anadromous phenotypes may coexist within a drainage system and form a single polytypic species (Ferguson 1989). In wild populations of brown trout within coastal river systems, freshwater (FW) residents, as well as anadromous individuals, may develop within the same genetic population (L'Abée-Lund et al. 1989; Hindar et al. 1991). This becomes obvious during springtime when the population differentiates into FW-resident and migratory fractions (Nielsen et al. 2006). At the age of 1–2 years, anadromous individuals undergo the process of

Received 10 August 2006. Accepted 2 March 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 16 June 2007. J19480

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 doi:10.1139/F07-059 © 2007 NRC Canada

parr–smolt transformation, which prepares the fish for the osmoregulatory and metabolic challenges in the new environment (see Hoar 1988). The main downstream smolt run in Danish rivers occurs between mid-March and mid-May (Rasmussen 1986). Once entering the ocean, the smolts are able to hypo-osmoregulate and utilize the abundance of food to optimise growth until returning as mature individuals to spawn in their native river (Klemetsen et al. 2003).

A variation to this life cycle is commonly seen in anadromous brown trout populations. Immature sea-run individuals may come back into freshwater during the winter months (November–March) and take up temporary residence in lower parts of the river. It is unknown to what degree they reside in their native river. In Denmark, these silvery fish are termed "Greenlanders" by laymen because of their resemblance to sea-run Greenlandic Arctic char (*Salvelinus alpinus*). In certain rivers they may be quite abundant during a few months and thus make an attractive recreational fishery. The trout (both sexes, 30–50 cm) have typically spent 0.5–2 years in the sea and re-enter the rivers with undeveloped gonads; thus the purpose of migration is obviously not spawning. The duration of the stay in freshwater is unknown, but judged by catch reports from anglers, they seem to descend the rivers again in March–April. The drive for the migration from the sea into freshwater is unknown but may be caused by a reduced hypo-osmoregulatory capacity when seawater (SW) temperatures drop to a critical low level. This is supported by laymen observations of higher abundance of ascending sea-run fish in cold winters and in those rivers flowing into high-salinity areas around Denmark compared with rivers flowing into low-salinity areas. However, not all immature fish leave the ocean, so there may also be genetic, nutritional, and local factors influencing the behaviour. Reduced hypo-osmoregulatory capacity at low temperature has been observed in Atlantic salmon (*Salmo salar*) smolts by Arnesen et al. (1998) and Handeland et al. (2000) and in rainbow trout (*Oncorhynchus mykiss*) by Finstad et al. (1988). Increased mortality and plasma osmolality and a general extension of the SW-acclimation period at low temperature were evident in those studies. To our knowledge, the consecutive influence of low temperature and high salinity has not been investigated in immature sea-run brown trout or any other salmonid.

Branchial ion regulation in FW and SW teleosts has been investigated in much detail in recent years, and several cellular and molecular components have been characterised (see Evans et al. 2005). In short, monovalent ion regulation at both salinities involves active, as well as passive, transport components that secure net ion uptake in FW and ion secretion in SW through cellular organisation. The major active transport component in both cases is a basolateral Na^+,K^+-ATPase enzyme that establishes electrochemical gradients of Na^+ and K^+ that may be utilized by secondary active ion-transport proteins to allow net uptake or secretion of Na^+ and Cl^-. There is some dispute about to what extent these mechanisms are placed in distinct branchial cells in euryhaline fish or whether some degree of molecular rearrangement may occur in certain cells (chloride cells) during salinity shifts, leading to a reversal in net ion-transport direction (see Evans et al. 2005). Temperature is an important determinant of the rate of ion transport; however, active and diffusive-exchange transport may be differently affected by different temperature coefficients (Raynard and Cossins 1991; Cossins et al. 1995). At low temperature, the rate of active mechanisms may be reduced more than that of passive mechanisms, leading to an overall disruption of ionic homeostasis. To maintain ion balance, some kind of molecular compensation is therefore needed. This may involve homeoviscous adaptation of membrane fluidity affecting permeability, adjustment of turnover rate, or de novo synthesis of particular ion-transport proteins. This acclimation process requires energy and may thus depend on the metabolic status of the animal (Hazel 1984; Hochachaka 1988).

The aim of the study was to investigate the hypo-osmoregulatory capacity at low temperatures of wild immature sea-run trout overwintering in freshwater and to investigate the timing of ocean re-entry of acoustic-tagged wild fish from the river in relation to time of day, body size, temperature, and water discharge.

Materials and methods

Study area

The present investigation included a field study of migratory behaviour and a laboratory study of the physiology of SW acclimation at low temperature. The field study was done in 2004 with wild fish from the River Ribe (Jutland, Denmark), which flows into the Wadden Sea (salinity 33 ppt; Fig. 1*a*). The laboratory study was performed in 2005 with fish from the River Ribe and the River Grenaa (Jutland, Denmark). The River Grenaa flows into the Kattegat Sea (salinity 25 ppt).

Field study

Twenty-eight immature, silvery sea trout (*Salmo trutta*; mean total length ± standard error of the mean (SEM) = 396 ± 17.5 mm) were caught in February 2004 by electrofishing (6000 W) in the River Ribe ca. 6 km from the river mouth (Fig. 1*b*). They were tagged with acoustic transmitters (weight 4.7 g, life expectancy of 240 days, range < 500 m; V8SC-2L R256, VEMCO, Shad Bay, N.S., Canada) during anaesthesia in 0.3 ppt 2-phenoxyethanol. The transmitters were inserted surgically into the abdominal cavity and the incision (10–14 mm) was closed with 1–2 stitches. After recovery the fish were released into the river. Five datalogger stations (VEMCO VR 2) were placed in the lower part of the river to detect downstream movement of the fish (Fig. 1*b*).

Laboratory study

Nonmature, silvery sea trout were caught by electrofishing (6000 W) on several occasions in the lower parts of the River Grenaa (4, 6, 8, 18, and 20 January 2005) and the River Ribe (15 and 17 February 2005) and transported in oxygenated water to the Danish Institute for Fisheries Research (Silkeborg, Denmark). Upon arrival, the fish were tagged for individual recognition with PIT (passive integrated transponder) tags during anaesthesia in 0.3 ppt 2-phenoxyethanol and transferred to a 2000 L flow-through tank with freshwater at the river temperature (3 °C). The fish were held at 3 °C for 1–17 days depending on catch date. Then the temperature was raised gradually to 10 °C over a 3-day period, and the fish

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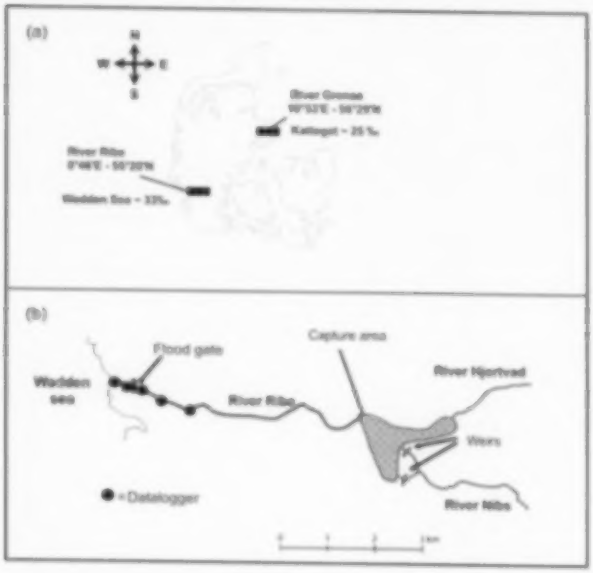
Fig. 1. (*a*) Location of Rivers Grenaa and Ribe in Denmark and the average salinity of the surrounding coastal areas. (*b*) Map of the lower part of River Ribe. The capture area for the fish and the location of the dataloggers are shown.



were held for an additional 24 h at 10 °C before further experimentation. The light cycle was 10 h light – 14 h dark. Food was withheld during the experiment.

Two separate experiments were conducted with fish from the two rivers. In each case, fish were randomly distributed to treatment groups. For River Grenaa, 39 fish were used (mean fork length ± SEM, 331.7 ± 10.1 mm; mean weight ± SEM, 335.6 ± 32.6 g), and for River Ribe, 43 fish were used (mean fork length, 357.3 ± 6.9 mm; mean weight, 478.8 ± 31.5 g). The experimental protocol was similar in the two experiments. After acclimation to FW – 10 °C, an initial sample (see below) was taken from all fish (S1). Two groups of fish were then transferred to 350 L tanks supplied with 33 ppt SW (10 °C) or FW (10 °C), and blood and gill biopsies were sampled 5 days after transfer (S2). The water temperature was then lowered from 10 °C to 2 °C over 4 days and serial sampling of the same individuals was performed at 3, 7, and 10 days after temperature lowering was completed (S3, S4, S5). Control groups were maintained in separate 350 L tanks in FW at both 10 °C and 2 °C and in SW at 10 °C, and these were sampled at the same time points. The number of fish sampled on the different occasions were as follows: at River Grenaa: FW – 2 °C, $n = 9$; FW – 10 °C, $n = 9$; SW – 2 °C, $n = 11$ (except for S3–S5 where $n = 10$); SW – 10 °C, $n = 11$ (except for S3 where $n = 10$ and S4–S5 where $n = 9$); River Ribe: FW – 2 °C, $n = 9$; FW – 10 °C, $n = 9$; SW – 2 °C, $n = 12$; SW – 10 °C, $n = 12$.

Sampling

The experimental procedures used in this study conform to local ethical requirements. For each sampling the following procedure was followed. Each fish was anesthetized in 0.3 ppt 2-phenoxyethanol, scanned for individual recognition, and weighed. A blood sample (100 µL, except 300 µL at S5) was drawn from the caudal vessels into a heparinized syringe and centrifuged at 5000*g* for 3 min. The plasma was transferred to a separate tube and frozen. Gill biopsies were taken by carefully excising the tips of 7–8 gill filaments (approximately one-third of the filament length) from the first gill arch. Some of these were frozen in liquid nitrogen in SEI buffer (300 mmol sucrose·L^{-1}, 20 mmol EDTA·L^{-1}, 50 mmol imidazole·L^{-1}; pH 7.3) for enzymatic analysis and some were placed in 100 µL RNAlater (Qiagen, Hilden, Germany) for mRNA analyses. Plasma and SEI-buffered gill samples were stored at –80 °C until analyses. Samples in RNAlater were stored overnight at 4 °C and then stored at –20 °C until analysed. After the final sampling (S5), the fish were stunned by a blow to the head and killed by brain pithing. The sex was determined and the gonads were taken out and weighed.

Analyses

Plasma osmolality was measured by vapour pressure osmometry on undiluted samples (Wescor, Logan, Utah). Plasma [Mg^{2+}] and [Ca^{2+}] were measured by atomic absorption spectrophotometry on samples diluted in 0.1% La_2O_3. Na^+,K^+-ATPase activity was analysed at 25 °C in crude homogenates of gill tissue by the semi-micro-coupled assay of McCormick (1993) by using a plate reader (Spectramax Plus, Molecular Devices, Sunnyvale, California). Protein content in gill homogenates was measured by the method of Lowry et al. (1951) modified for plate reader. The relationship between ATP hydrolysis and ΔOD_{340} was determined experimentally in a calibration assay, and the enzymatic activities were calculated as micromoles of ADP per milligram of protein per hour.

RNA isolation and quantitative PCR

Total RNA was isolated from gill tissue stored in RNAlater by the Trizol method according to the manufacturer's manual (Invitrogen, Carlsbad, California). The purity was checked by the A_{260}–A_{280} ratio, which was always 1.6–1.8. Following isolation, RNA was quantified using a RiboGreen RNA Quantitation Kit (Molecular Probes, Eugene, Oregon) according to the manufacturer's manual. First-strand complementary DNA (cDNA) was synthesized from 1 µg total RNA following the instructions of the SuperScript II RNase H$^-$ Reverse Transcriptase Kit (Invitrogen, Carlsbad, California). Expression of Na^+,K^+-ATPase α1a and α1b subunit isoforms was investigated using SYBR-based quantitative polymerase chain reaction (qPCR) analysis using the isoform-specific primers for *O. mykiss* Na^+,K^+-ATPase α1a and α1b subunits published by Richards et al. (2003). Gene-specific expression was normalised to expression of elongation factor 1α (EF-1α; accession No. AF321836) using the following primers: forward, 5′-GAGAACCATTGAGAAGTTCGAGAAG-3′; reverse, 5′-GCACCCAGGCATACTTGAAAG-3′. PCRs were done with Brilliant SYBR Green QPCR Master Mix (Stratagene, La Jolla, California) on a Mx3000P (Stratagene, California). PCRs contained 1 µL cDNA (50 ng RNA), 150 nmol·L^{-1} of each primer, and 12.5 µL Brilliant SYBR Green QPCR Master Mix in a total volume of 25 µL. For each analysis, a NTC (no template control) was included. All qPCRs were performed as follows: 10 min of polymerase activation at 95 °C

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followed by 40 cycles of 95 °C for 30 s and 60 °C for 1 min. Melting curve analysis was performed following each reaction to confirm the presence of only a single product of the reaction. In addition, representative PCR products were analysed by electrophoresis to verify that only a single band was present. Negative control reactions were performed for representative samples using RNA that had not been reverse-transcribed to control for the possible presence of genomic DNA contamination. Genomic DNA was present but never constituted more than 1:32768. NTC reactions were also performed to verify that there was no cDNA contamination or primer–dimer amplification in the reactions. The results were normalized to EF-1α by the $\Delta\Delta C_T$ method (Livak and Schmittgen 2001), and results are presented as arbitrary numbers.

Statistics

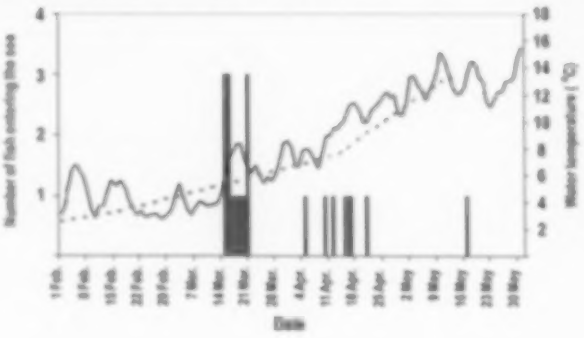
To investigate the effect of the experimental procedure (captivity and sampling) on plasma osmolality and gill Na^+,K^+-ATPase activity, all data were analysed using a repeated-measures analysis of variance (RM-ANOVA) with two within-subject factors (i.e., five Na^+,K^+-ATPase activity and five plasma osmolality at 10 °C and FW) using repeated-contrast design. RM-ANOVA with backward elimination was preferred before a profile analysis because the latter has lower power (Maxwell and Delaney 1990; Potvin et al. 1990). If data did not meet the "sphericity assumption" (Mauchly's test of sphericity), then the number of degrees of freedom was reduced with a Huynh–Feldt epsilon (von Ende 1993). Data were log-transformed to meet the demands of the ANOVA assumption of homogeneity of variances. All post hoc tests were Bonferroni-adjusted according to recommendations by Day and Quinn (1989). The effects of temperature (2 and 10 °C), salinity (0 and 33 ppt), gender, weight, and length on plasma osmolality and gill Na^+,K^+-ATPase activity were analysed using RM-ANOVA with two within-subject factors (i.e., three Na^+,K^+-ATPase activity and three plasma osmolality measurements) using repeated-contrast design. Further analysis followed the above-mentioned procedure. Effects of salinity and temperature on Na^+,K^+-ATPase mRNA expression and plasma $[Mg^{2+}]$ and $[Ca^{2+}]$ was examined at S5 using a two-way ANOVA followed by a Bonferroni test. The statistical analyses were performed using SPSS 10.05 (SPSS Inc., Chicago, Illinois) and Prism 3.03 (GraphPad Software, San Diego, California).

Results

Field study

Twenty-one out of 28 tagged fish left the River Ribe and returned to the ocean. Nineteen returned between 15 March and 21 April 21 2004 (Fig. 2), one returned 17 May 2004, and one, 16 March 2005. The latter is not included in the analysis. The fate of the remaining seven fish is unknown. Downstream movement was initiated when river and coastal water temperature increased above 6 °C (Fig. 2) and was not related to water discharge (not shown). There was no statistical relationship between date of downstream movement and size of the fish (linear regression, $P = 0.81$). Datalogger passages were evenly distributed over the day (Rayleigh test, $P = 0.99$).

Fig. 2. Descent of immature, tagged fish into the sea (vertical bars) in relation to water temperature in River Ribe (solid line) and in the coastal water (broken line).



Laboratory study

Upon capture, very few fish had marine parasites attached. No data were recorded from River Grenaa; from River Ribe, one fish (out of 43) had sea lice and six had leaches. These data did not correlate with other parameters measured and could not be used for estimating residence time in FW. There was zero mortality in FW fish from River Grenaa throughout the holding, acclimation, and experimental period. In the group exposed to SW at 10 °C, the cumulated mortality was 18% at S5. Fish in SW at 2 °C experienced 9% mortality. There was zero mortality before and during the River Ribe experiment.

Plasma osmolality (Fig. 3) increased after transfer from FW to SW at 10 °C (S2) in fish from both rivers. Twelve days after transfer (S3), plasma osmolality was regulated to a lower level but still higher than FW controls from River Grenaa. There was no significant change ($P > 0.05$) in the FW – 10 °C group from River Grenaa but plasma osmolality decreased significantly over time in River Ribe fish ($P < 0.001$). In fish from River Grenaa, lowering of the temperature from 10 to 2 °C caused a marked increase in plasma osmolality in the SW group, and there was a significant interaction between temperature and salinity. A similar response was observed in the River Ribe fish, although the increase in plasma osmolality was smaller.

There was an overall effect of salinity ($P < 0.0001$) and temperature ($P < 0.007$) (interaction, $P < 0.0003$) on plasma $[Mg^{2+}]$ in River Grenaa fish, which was higher in the SW – 2 °C group compared with SW – 10 °C and FW – 2 °C groups (Fig. 4*a*). In River Ribe fish, there was an overall effect of salinity ($P < 0.0001$) and temperature ($P < 0.019$) on plasma $[Mg^{2+}]$, which was significantly higher in both SW groups compared with the corresponding FW controls (no interaction; Fig. 4*b*). There was no effect of salinity or temperature on plasma $[Ca^{2+}]$ in fish from both rivers (Fig. 5).

Exposure to SW at 10 °C caused an increase in gill Na^+,K^+-ATPase activity in fish from both rivers at S3, after which activity was relatively constant (Fig. 6). Enzyme activity in the SW – 2 °C groups was similar to that in the SW –10 °C groups for River Grenaa fish. In fish from River Ribe, there was a significant interaction between temperature and salinity ($P = 0.003$). There was a significant decrease in gill Na^+,K^+-ATPase activity over time in the FW control groups

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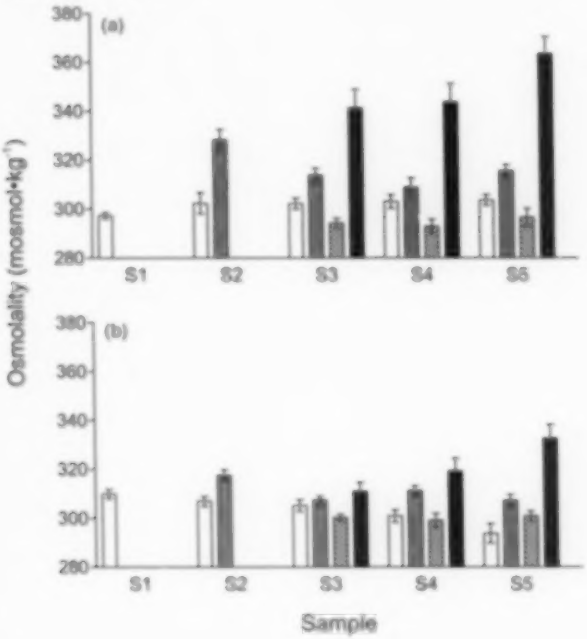
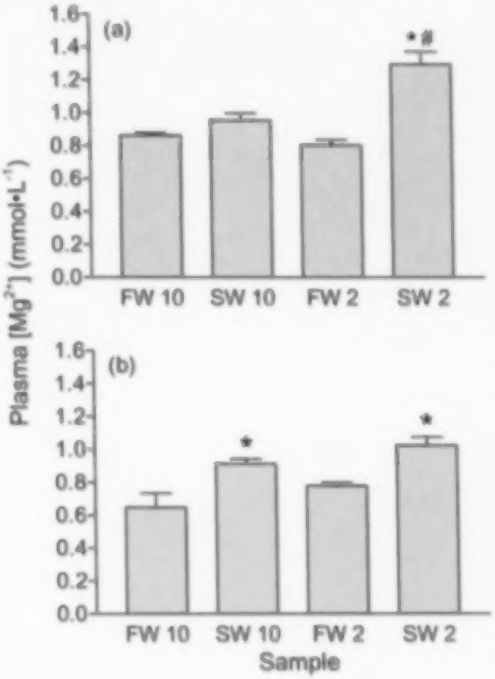
Fig. 3. Effect of seawater (SW) transfer (33 ppt) and temperature (2 and 10 °C) on plasma osmolality in immature *Salmo trutta* from (*a*) River Grenaa and (*b*) River Ribe. Values are mean ± standard error of the mean (n = 9–12). A significant effect of time was found in the freshwater (FW) 10 °C group from River Ribe ($P < 0.001$, repeated-measures analysis of variance, RM-ANOVA), but the test could not locate the difference between any of the four "within-subject contrast levels" ($P > 0.219$). SW exposure elevated plasma osmolality in fish from both rivers, and there was a significant interaction (RM-ANOVA: River Grenaa, $P < 0.0001$; River Ribe, $P < 0.025$) between temperature and salinity, causing an additional increase in plasma osmolality. Open bars, FW – 10 °C; shaded bars, SW – 10 °C; cross-hatched bars, FW – 2 °C; solid bars, SW – 2 °C.



(10 °C) from both rivers ($P < 0.01$). The activity in the FW – 2 °C groups remained at a level close to the initial activity in River Ribe fish, whereas there was a decrease in enzyme activity at S5 in River Grenaa fish. In fish from both rivers, enzyme activity in FW – 2 °C groups was slightly elevated compared with that in FW – 10 °C groups.

At the terminal sampling (S5), there was an overall effect of salinity ($P < 0.0002$) on gill α1a Na^+,K^+-ATPase mRNA in fish from River Grenaa. FW levels were higher than SW levels at both temperatures (Fig. 7*a*). There was no overall effect of temperature, but low temperature tended to elevate mRNA levels further ($P < 0.066$). The same pattern was observed for the fish from River Ribe ($P < 0.0001$) (Fig. 8*a*). Salinity ($P < 0.0001$) and temperature ($P < 0.0056$) had overall effects on α1b Na^+,K^+-ATPase mRNA in River Grenaa fish (interaction, $P < 0.0013$; Fig. 7*b*). The level was higher in SW – 2 °C groups than in SW – 10 °C and FW – 2 °C groups. In the River Ribe fish, there was an overall effect of salinity ($P < 0.0001$), with the level of gill α1b Na^+,K^+-ATPase mRNA being significantly higher in SW groups than in the corresponding FW groups (Fig. 8*b*).

Fig. 4. Effect of seawater (SW) transfer (33 ppt) and temperature (2 and 10 °C) on plasma [Mg^{2+}] in immature *Salmo trutta* from (*a*) River Grenaa and (*b*) River Ribe. Values are mean ± standard error of the mean (n = 9–12). An asterisk (*) indicates an effect of salinity at that time at a given temperature ($P < 0.05$); "#" indicates an effect of temperature at a given salinity ($P < 0.05$). SW exposure overall elevated plasma [Mg^{2+}].



Discussion

Osmoregulation

Following transfer of FW-acclimated trout to 33 ppt SW, there was 18% and 9% mortality among fish from River Grenaa at 10 and 2 °C, respectively, and no mortality among fish from River Ribe. This indicates that River Ribe fish, which ascend from a high-salinity coastal area, are better able to re-activate hypo-osmoregulatory mechanisms after a short residence in FW during winter compared with River Grenaa fish, which ascend from a 25 ppt coastal area. Local adaptation and (or) differences in biotic factors (food availability, metabolic status, etc.) may explain this difference between stocks. Among survivors at 10 °C from both stocks, plasma osmolality increased transiently and was stabilised at a level only slightly higher than that of FW controls. A temperature drop from 10 °C to 2 °C caused a sustained increase in plasma osmolality in fish from both stocks. River Grenaa fish showed the largest increase, approaching 370 mosmol·kg^{-1} after 10 days, again indicating a poorer ability to reactivate hypo-osmoregulatory mechanisms in this stock. The level of 370 mosmol·kg^{-1} is tolerable but not preferable in the long run. This effect of low SW temperature is similar to that observed in Atlantic salmon smolts (Sigholt and Finstad 1990; Arnesen et al. 1998; Staurnes et

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Fig. 5. Effect of seawater (SW) transfer (33 ppt) and temperature (2 and 10 °C) on plasma $[Ca^{2+}]$ in immature *Salmo trutta* from (*a*) River Grenaa and (*b*) River Ribe. Values are mean ± standard error of the mean (n = 9–12). There was no effect of temperature or salinity on plasma $[Ca^{2+}]$.

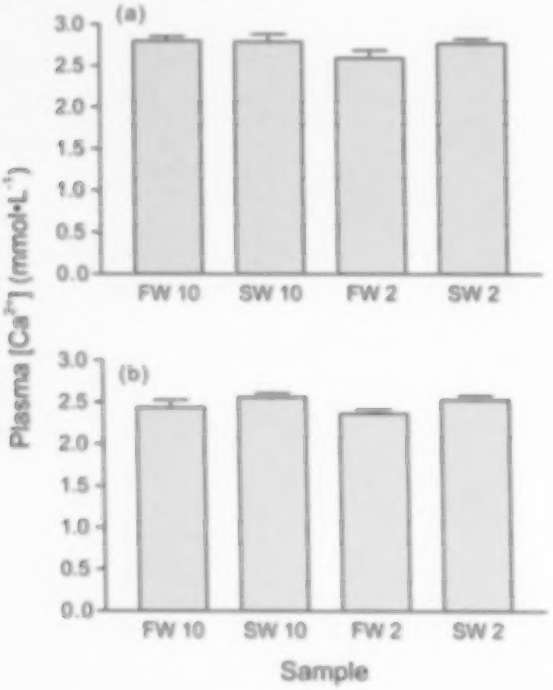
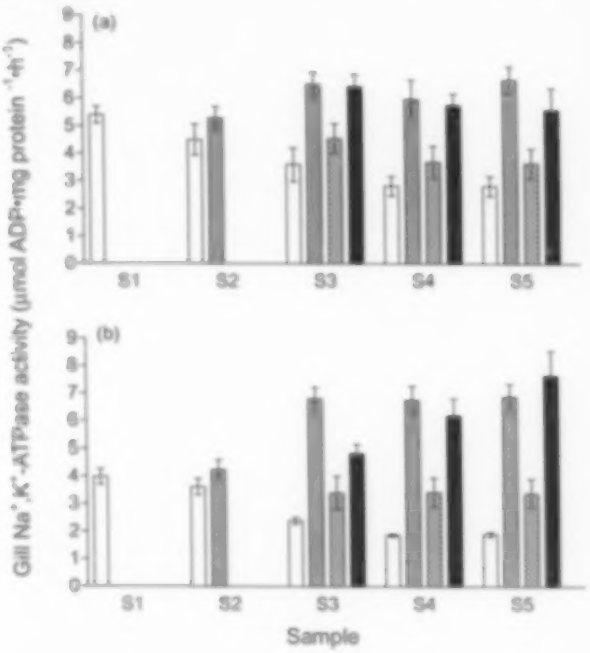


Fig. 6. Effect of seawater (SW) transfer (33 ppt) and temperature (2 and 10 °C) on gill Na^+,K^+-ATPase activity in immature *Salmo trutta* from (*a*) River Grenaa and (*b*) River Ribe. Values are mean ± standard error of the mean (n = 9–12). There was a significant effect of time in the freshwater (FW) 10 °C group in River Grenaa (repeated-measures analysis of variance (RM-ANOVA), $P < 0.001$), but the difference was not found from one sampling to the next. A significant difference was found between samplings S2 and S3 in the FW –10 °C group in River Ribe (RM-ANOVA, within subject level, $P < 0.05$). Open bars, FW – 10 °C; shaded bars, SW – 10 °C; cross-hatched bars, FW – 2 °C; solid bars, SW – 2 °C.



al. 2001) and in rainbow trout (Finstad et al. 1988; Belkovskii et al. 1991). Arnesen et al. (1998) and Staurnes et al. (2001) changed salinity and tested temperature in one step, which may have impaired the ability to acclimate. In our study, the fish were acclimated to SW at 10 °C before lowering the temperature, thereby allowing them to acclimate to one parameter at a time. However, this did not seem to improve their performance. The elevation of plasma $[Mg^{2+}]$ but not plasma $[Ca^{2+}]$ in SW fish suggested that renal function was compromised at the low temperature.

Trout from both rivers displayed a relatively high mean gill Na^+,K^+-ATPase activity (>4 µmol ADP·mg protein^{-1}·h^{-1}) at the time of the first sampling, indicating that they had spent a relatively short time in the river, even though trout from two catch dates were pooled in this calculation. SW-acclimated brown trout typically have gill Na^+,K^+-ATPase activity around 6–10 µmol ADP·mg protein^{-1}·h^{-1} (S.S. Madsen, unpublished data), and fully FW-acclimated trout have values of 1–2 µmol ADP·mg protein^{-1}·h^{-1} outside the smolting peiod (Madsen et al. 1995; Seidelin et al. 2000; Tipsmark et al. 2002). The activity continually decreased during the 19 days of FW residence, suggesting loss of hypo-osmoregulatory capacity rather than loss of hyper-osmoregulatory capacity. This is in agreement with Tipsmark et al. (2002), who found a slow decrease in enzyme activity when trout were transferred from SW to FW. The decrease was less pronounced in the FW – 2 °C groups, which may reflect a reduced protein turnover rate or a compensatory response to low temperature. Ion balance was only slightly affected by the reduced FW temperature. A compensatory increase in enzyme activity in response to cold acclimation has been reported in FW rainbow trout (McCarty and Houston 1977), goldfish (*Carrassius auratus*, Paxton and Umminger 1983), and FW Arctic char (Schwarzbaum et al. 1991) and may be part of the strategy to correct for ionic imbalances at low water temperatures. Upregulation of branchial V-type H^+-ATPase may also be expected to occur as part of the compensatory regulation of active ion uptake. Additionally, a reduction in cell membrane ionic permeability may contribute to balancing passive fluxes against active movement of monovalent ions (Hochachaka 1988; Cossins et al. 1995). Alternatively, the decreased enzyme activity observed during FW residency at 10 °C may be induced by the combination of food deprivation (Jürss et al. 1983) and elevated temperature (Aas-Hansen et al. 2003).

Gill Na^+,K^+-ATPase activity increased when trout were transferred to SW and reached a stable level 12 days after transfer (S3). This response is commonly seen when salmonids are acclimated to SW and reflects the develop-

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Fig. 7. Effect of seawater (SW) transfer and temperature (2 and 10 °C) on mRNA expression of (*a*) gill α1a and (*b*) gill α1b Na^+,K^+-ATPase subunits in immature *Salmo trutta* from River Grenaa at sampling S5. Expression was normalized to elongation factor 1α (EF-1α). Values are mean ± standard error of the mean ($n = 4$). An asterisk (*) indicates an effect of salinity at that time at a given temperature ($P < 0.05$); "#" indicates an effect of temperature at a given salinity ($P < 0.05$).

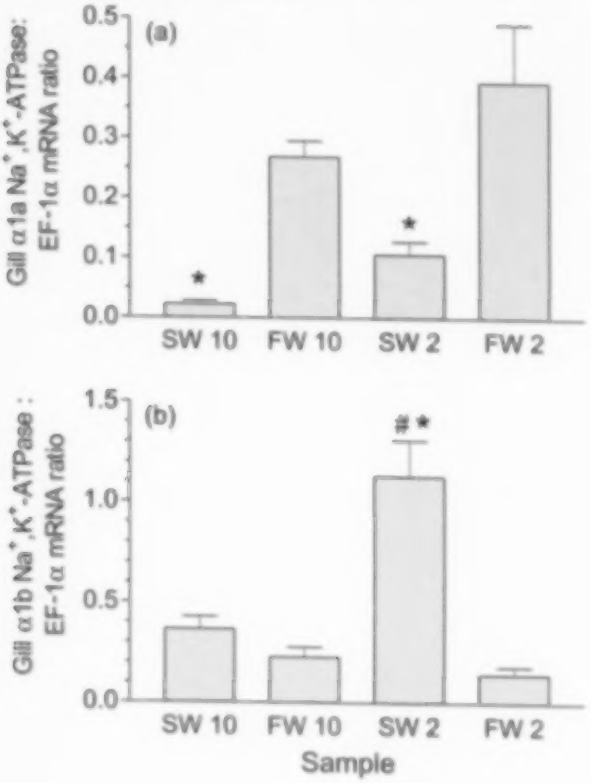
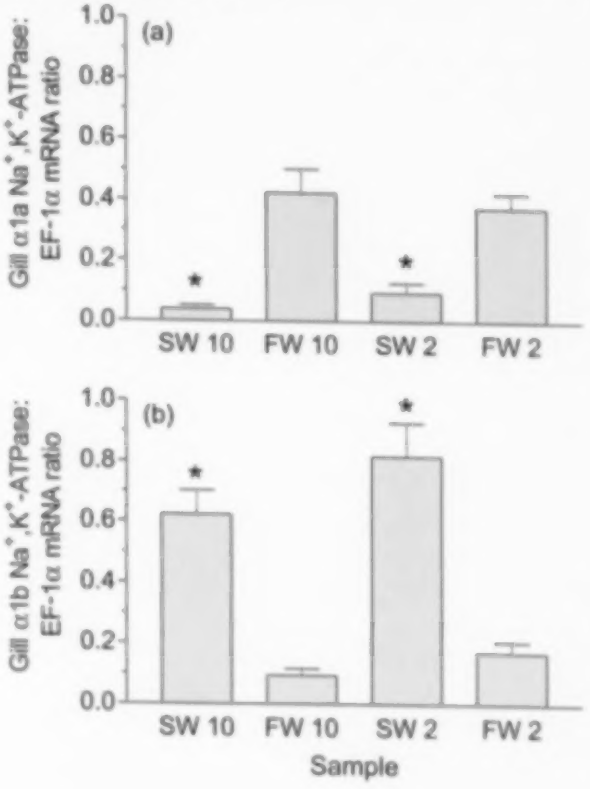


Fig. 8. Effect of seawater (SW) transfer and temperature (2 and 10 °C) on the mRNA expression of (*a*) gill α1a and (*b*) gill α1b Na^+,K^+-ATPase subunits in immature *Salmo trutta* from River Ribe at sampling S5. Expression was normalized to elongation factor 1α (EF-1α). Values are mean ± standard error of the mean ($n = 6$). An asterisk indicates an effect of salinity at that time at a given temperature ($P < 0.05$).



ment of hypo-osmoregulatory mechanisms in chloride cells of the filament area of the gill (Seidelin et al. 2000; Tipsmark et al. 2002). Because the enzymatic assay is run at optimal conditions, the mechanism for this increase may be de novo synthesis of functional pump units or increased turnover rate of pre-existing pumps. The relatively slow time course of stimulation suggests that de novo synthesis is the major factor involved. The intensity of stimulation was not affected by lowering the acclimation temperature to 2 °C. Thus when extrapolating from the assay temperature at 25 °C to the actual in vivo temperatures, lack of pumping capacity may be one explanation for the increasing ionic imbalance in the SW – 2 °C trout. A lack of compensatory response in active transport mechanisms in the gill supports Arnesen et al. (1998), who showed that gill Na^+,K^+-ATPase activity increased at a slower rate at 2 °C than at 6 °C after SW transfer of Atlantic salmon smolts, and Handeland et al. (2000), who found no change in gill Na^+,K^+-ATPase activity after SW transfer of smolts at 4.6 °C. Thus *Salmo* species may be unable to fully compensate for reduced SW temperature by an increase in gill Na^+,K^+-ATPase activity. As a result, ionic imbalance occurs when the temperature drops beyond a critical minimum (present study; Finstad et al. 1988; Arnesen et al. 1998; Handeland et al. 2000). By contrast, a compensatory increase in gill Na^+,K^+-ATPase activity is seen in cod (*Gadus morhua*) when transferred from 8 °C to 1 °C in SW (Staurnes et al. 1994). In addition to compensatory regulation of active transport components, passive ionic permeability may have been affected by the drop in temperature (Cossins et al. 1995). However, judging by the steadily increasing plasma osmolality, this is insufficient in the present experiment.

Na^+,K^+-ATPase is heavily involved in ion uptake, as well as ion secretion, in teleost gills. There is some dispute about which cell types host the bulk of enzyme in the different functions. Earlier salmonid studies have established that the overall abundance and activity of the enzyme and its two subunits increase during SW acclimation (D'Cotta et al. 2000; Singer et al. 2002). In addition, several studies have shown that α1 Na^+,K^+-ATPase mRNA increases after transfer to SW (Madsen et al. 1995; D'Cotta et al. 2000; Singer

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et al. 2002). More recently, the focus has turned to how isoform mRNA expression patterns in the gill are affected by salinity. Several α-subunit isoforms (α-1a, α-1b, α-1c, α3) have been identified in the gills of teleosts and may participate in different functions; their cellular location has yet to be determined. In our study, the α-1a isoform was expressed at a higher level in FW fish and the α-1b isoform was expressed at higher levels in SW fish at the terminal sampling (S5). This was also seen at S2, 5 days after SW transfer (not shown). These data are in accordance with the emerging picture of α-1a being the FW-type isoform and α-1b being the SW-type isoform in salmonids (Richards et al. 2003; Mackie et al. 2005). Alpha-1c and α-3 were not measured in the present study but may represent "housekeeping" isoforms with ubiquitous tissues distribution and largely unresponsive to salinity changes (Richards et al. 2003). Temperature had no effect on the expression of α-1a in fish from either both stocks or salinities. However, the α-1b isoform was expressed at significantly higher levels at the low temperature in SW in the River Grenaa fish, suggesting an increased effort by these fish to increase the ion-secretory capacity by increasing the amount of Na^+,K^+-ATPase enzyme.

Seaward migration during spring

Downstream movement of the majority of the River Ribe fish (13/21) occurred during a narrow time period between 15 and 21 March, coincident with a sudden increase in river temperature. By awaiting a temperature stimulus, ocean temperature may have reached a tolerable level. This is similar to smolt migration, which is triggered by elevated water temperature (Jonsson and Ruud-Hansen 1985) and to a lesser degree by water discharge (Hansen and Jonsson 1985) once a critical physiological threshold is reached. The movement of fish occurred at all times of day, which is opposed to the nocturnal migration of smolts. Nocturnal migration may protect smolts from the risk of predation (Moore et al. 1998); however, because of their bigger size and thus less risk of predation, descending overwintering sea trout move irrespective of time of day. Overwintering in FW and return to SW in the spring also occurs in adult immature Arctic char (Aas-Hansen et al. 2005). During the winter, Arctic char in FW has reduced gill Na^+,K^+-ATPase activity and hypo-osmoregulatory capacity, but both increase in the spring before migration (Aas-Hansen et al. 2005); thus in this species, resmoltification seems to occur. Gill Na^+,K^+-ATPase activity steadily decreased in trout held in FW in our study, suggesting loss of SW tolerance during FW residency. Nevertheless, hypo-osmoregulatory mechanisms were re-activated during SW challenge at all temperatures but only successfully at 10 °C. Future studies should investigate whether a smoltification-like transformation occurs in overwintering sea trout in advance of their return migration to the sea.

The drive for FW overwintering?

As reviewed by Klemetsen et al. (2003), the degree of life history variation in brown trout is among the highest seen in anadromous salmonids. Habitat shifts are common throughout life, both within the FW habitat and between FW, the estuary, and the sea. A central question of interest is why do such extensive habitat shifts and migrations occur in this species? The nearby answer is that the overall benefit–cost ratio is increased for the individual, which increases the evolutionary fitness of the species (Gross 1987). Increased food availability in the new habitat is one key factor that may drive diadromy (Gross 1987) when founded by genetic selection. In the case of overwintering sea trout, however, the majority of fish caught in the river had empty stomachs or very little evidence of feeding activity (A. Koed, unpublished data), which does not suggest that improved feeding options are exploited.

Physiological constraints in the present habitat may be a more direct drive in influencing the migratory behaviour. In brown trout, there is evidence of both genetic influence and phenotypic plasticity in life history tactics but the trade-offs are often confusing. For instance, the "choice" as juvenile between FW residency, smolting–anadromy, and maturation (mostly in males) is only to a certain degree influenced by heredity, as no "pure" anadromous strains have been described. The mechanisms regulating phenotypic variability at this stage are not understood. In the case of overwintering immature sea trout in the FW habitat, the present study asked the question of whether this strategy was driven by physiological constraints, mainly preprogrammed into the individual, or a combination of the two. Our data clearly reveal that the hypo-osmoregulatory capacity of overwintering trout caught in the river is compromised at low temperature. This is the case in so far as the combination is 33 ppt and 2 °C. Thus for sea trout living in high-salinity coastal areas (e.g., River Ribe), hypo-osmoregulatory problems may very well be the reason for the river ascend during winter. However, even though less frequently observed, immature trout living in low- to moderate-salinity areas also seek FW during winter (e.g., River Grenaa). It is unknown why not all fish in a given coastal population seek FW during winter. Knutsen et al. (2004) reported that immature sea trout of similar size to the ones in our study were caught feeding in coastal areas of the Skagerak (20–27 ppt) at low temperatures (3–10 °C) during winter. Those fish that seek FW during winter may represent particularly sensitive individuals, but it cannot be excluded that overwintering also reflects the general phenotypic plasticity of this species. The phenomenon should be viewed as yet an alternative life strategy in anadromous brown trout, similar to that occurring at earlier stages when residency, early maturation, and anadromy are the "options". To reveal this, the ideal experiment would be to analyse physiological differences between potential Greenlanders and resident SW fish caught at sea before river ascend is initiated.

In conclusion, sea-run FW-acclimated brown trout were able to re-acclimate to full-strength SW at 10 °C during winter. At 2 °C this capacity was compromised, though not fatally within the observation period. Our data give support to the view that anadromous brown trout living in high-salinity coastal regions may use the FW habitat as an osmoregulatory refuge during extreme winters. It is, however, unknown to what degree these fish would be challenged by salinities < 25 ppt. River Ribe fish performed better than River Grenaa fish, so even though more data would be favourable to strengthen this conclusion, the data suggest that local adaptation may have improved the ability to handle the combination of high salinity and low water temperature.

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Acknowledgements

This study was funded by the Danish Rod and Net Fish License Funds. S.S.M was supported by a grant from the Danish National Science Research Council (21-02-0520).

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The effects of hatchery domestication on competitive dominance of juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: We tested the null hypotheses that competitive dominance among juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in contest and scramble experiments would not be affected by domestication selection after one generation of state-of-the-art hatchery culture. Dyadic challenges of size-matched juvenile fish were conducted after a 6-day acclimation in 113.4 L aquaria. Differences in dominance and frequency of different types of agonistic interactions used were not significantly different in contest ($n = 505$) or scramble ($n = 363$) competition experiments ($P > 0.05$). However, wild origin fish were more aggressive than hatchery origin fish in both types of experiments ($P \leq 0.05$). Furthermore, wild origin fish gained more weight than hatchery origin fish during contest experiments, and hatchery origin fish lost less weight than wild origin fish in scramble experiments ($P \leq 0.05$). Dominant fish, regardless of origin, grew more than subordinate fish in both contest and scramble experiments ($P \leq 0.05$). Our results indicate that aggression, and growth mediated by competition, can be affected by domestication after only one generation of state-of-the-art hatchery culture; however, impacts to competitive dominance appear to be small.

Résumé : Nous testons les hypothèses nulles qui veulent que la dominance de compétition chez de jeunes saumons chinook (*Oncorhynchus tshawytscha*) dans des expériences de compétition de combat et de mêlée ne soit pas affectée par la sélection due à la domestication après une génération d'élevage dans une pisciculture de pointe. Nous avons organisé des confrontations dyadiques de jeunes poissons appariés en fonction de la taille après 6 jours d'acclimatation dans des aquariums de 113,4 L. Les différences dans la dominance et dans la fréquence des diverses interactions agonistes ne sont pas significativement ($P > 0,05$) distinctes dans les expériences de compétition de combat ($n = 505$) et de mêlée ($n = 363$). Cependant, les poissons d'origine sauvage sont plus agressifs ($P \leq 0,05$) que les poissons d'élevage dans les deux types d'expériences. De plus, les poissons d'origine sauvage accumulent plus de masse que les poissons d'élevage au cours des expériences de combat et les poissons d'élevage perdent moins de masse que les poissons sauvages dans les expériences de mêlée ($P \leq 0,05$). Les poissons dominants, quelle que soit leur origine, croissent plus rapidement que les poissons subordonnés, tant dans les expériences de combat que de mêlée ($P \leq 0,05$). Nos résultats indiquent que l'agressivité et la croissance sous le contrôle de la compétition peuvent être affectées après une seule génération d'élevage dans une pisciculture de pointe; les effets sur la dominance de compétition semblent, cependant, être limités.

[Traduit par la Rédaction]

Introduction

Despite our best efforts, raising fish in hatcheries may cause unintended behavioral changes in salmonids because of domestication selection, but no studies have evaluated whether our best efforts reduce behavioral changes. Domestication is defined as natural selection in artificial environments (Campton 1995). Selection in artificial environments could be due to intentional or artificial selection, biased sampling during some stage of culture, or unintentional selection (Busack and Currens 1995). The goal of supplementation or conservation hatcheries is to produce fish that will integrate well into natural populations (Mobrand et al. 2005). Managers of conservation hatcheries attempt to minimize intentional or biased sampling so that the hatchery fish are genetically similar to naturally produced fish. However, the selective pressures in hatcheries are dramatically different than in the natural environment, which can result in genetic differences between hatchery and wild fish (Reisenbichler and McIntyre 1977; Einum and Fleming 2001; Weber and Fausch 2003) and subsequently differences in behavior (Berejikian et al. 1996; Metcalfe et al. 2003; Wessel et al. 2006). The selective pressures may be particularly prominent during the freshwater rearing stage where substantial mortality of wild fish occurs (Groot and Margolis 1991).

Received 10 April 2006. Accepted 5 March 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 19 June 2007. J19268

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 doi:10.1139/F07-058 © 2007 NRC Canada

During freshwater rearing, salmonids in hatcheries and rivers use very different methods to acquire food. River environments are heterogenous with respect to food and habitat quality. Salmonids rearing in streams primarily feed on drifting invertebrates as they maintain energetically profitable stream locations (Fausch 1984). Dominant fish secure the most food and often grow the fastest (Metcalfe 1986). These fish use a variety of agonistic interactions, such as nips, butts, chases, and threats to defend territories that have predictably high levels of food (Chapman 1962; Grant and Kramer 1990; McMichael et al. 1999). This type of interaction is referred to as contest or interference competition (Birch 1957). Salmonids in hatchery raceways live in homogenous environments and at high densities where defending distinct territories may not be advantageous or even possible (Maynard et al. 1995). Fish in hatcheries frequently use shoaling or schooling behaviors and acquire food from the water surface (Weber and Fausch 2003). Thus, agonistic interactions prior to feeding may waste energy, but result in few immediate negative consequences (e.g., reduced growth, reduced survival) in hatchery environments, where food is plentiful and predators absent (Maynard et al. 1995; Einum and Fleming 2001). Fish that are in the right place at the right time and that swim rapidly towards the food are the most successful. This type of interaction is referred to as scramble or exploitative competition (Birch 1957). Exploitative competition may also occur in natural environments, particularly when space is not limited but fish densities are sufficiently high, fish densities are so high that territorial behavior is unprofitable, aggression levels are low, or locally abundant sources of food are unpredictable (Rodriguez 1995; Grant and Imre 2005).

Domestication selection has been shown to alter the aggressiveness and dominance of hatchery fish. For example, domestication has been implicated as causing either an increase, no change, or decrease in aggressive and schooling behavior in fish (Ruzzante 1994; Einum and Fleming 2001). Berejikian et al. (1996) found that offspring of wild steelhead trout (sea-run *Oncorhynchus mykiss*) were initially more aggressive and dominant than size-matched offspring of parents that had been in hatchery culture for four to seven generations. However, when hatchery fry had a 3.0%–4.5% size advantage, they dominated wild fish in 68% of encounters. Swain and Riddell (1990) found that domesticated coho salmon (*Oncorhynchus kisutch*) were more aggressive than those of natural origin from nearby streams. Three domesticated stocks of Atlantic salmon (*Salmo salar*) were generally dominant over wild origin juveniles when both had been raised in a common hatchery environment; however, when wild origin fish were given a 2-day period of prior residence, the asymmetry in dominance was reversed (Metcalfe et al. 2003). Petersson and Jarvi (2000) suggested that both contest and scramble competition affected the growth of brown trout (*Salmo trutta*) parr of natural and sea-ranched origins. Farrell (2003) found that wild spring Chinook salmon (*Oncorhynchus tshawytscha*) from the Yakima Basin were competitively dominant to descendents of first generation, local origin hatchery fish in a contest competition experiment during 2002.

The goals of this study were to determine if there are differences in dominance between offspring of wild and first generation hatchery spring Chinook salmon from the upper Yakima Basin under (*i*) contest and (*ii*) scramble competition. If domestication has not occurred, we would expect offspring of hatchery and wild fish to have equivalent levels of aggression and dominance. If domestication has occurred, we would expect offspring of hatchery fish to be dominant in scramble competition and offspring of wild fish to be dominant in contest competition. We also conducted a separate growth experiment to determine if differences in growth in the competition trials could be attributed to inherent capabilities to grow caused by domestication.

Materials and methods

Fish used in this experiment were juvenile offspring of either wild spring Chinook salmon or offspring of fish that were spawned artificially in the hatchery, reared to smolt, and released. As such, these fish were neither truly hatchery nor wild fish because they were not produced in the natural environment or with conventional hatchery practices (e.g., reared in circular tanks, not concrete raceways). However, for the ease of communication we refer to offspring of wild spring Chinook salmon as wild, and the offspring of fish that were spawned artificially in the hatchery, reared, and released as smolts are referred to as hatchery. The fish that spent one generation in the hatchery were offspring of wild spring Chinook salmon that were collected at Roza Dam, located in central Washington, as part of the Yakima/Klickitat Fisheries Project Supplementation Program. The only difference between the two types of fish was that the hatchery fish spent a portion of one generation in the hatchery. The hatchery fish were treated using state-of-the-art fish culture practices. For example, natural origin adult fish were collected in proportion to their abundance and timing at Roza Adult Monitoring Facility, located at Roza Dam, and a factorial mating design (e.g., 2 × 2 or 3 × 3) was used to increase the genetic diversity of the offspring. Adult fish that were taken to the hatchery were held in ponds, spawned, their eggs incubated, and juveniles reared in raceways (30.5 m long × 3.0 m wide × 1.1 m water deep) containing densities of approximately 40 000 fish per raceway.

Parental fish used for this experiment were collected, held, and spawned in the same way as previously described for the hatchery. Naturally produced fish were spawned with naturally produced fish to produce wild fish, and hatchery fish were spawned with hatchery fish to produce hatchery fish. After spawning, fertilized eggs were disinfected and placed in small cylindrical containers (isolettes; 10.2 cm in diameter and 5 cm tall), within incubation trays as a means to identify individual families. Isolettes were selected in a way that ensured nearly all adult broodstock used for the experimental isolette crosses were represented in our sample at least once (wild females: 33 (2003), 18 (2004); wild males: 25 (2003), 18 (2004); hatchery females: 32 (2003), 20 (2004); hatchery males: 15 (2003), 20 (2004); wild families: 58 (2003), 54 (2004); hatchery families: 59 (2003), 58 (2004)). Hatchery and wild fish were transferred to two identical 1710 L polyethylene, conical-bottomed circular tanks on 17 April 2003 and 19 April 2004 and then fed starter feed until large enough to feed on Bio-Oregon moist pellets. Circular tanks were exposed to natural light and

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were supplied with water from the same source as the hatchery (i.e., mostly Yakima River water).

Experiments were conducted in eighty 113.4 L glass aquaria (91.4 cm long, 30.5 cm wide, 40.6 cm deep inside dimensions) at the Cle Elum Supplementation and Research Facility, located in the upper Yakima Basin near the town of Cle Elum, Washington. Experiments were initiated when fish were large enough to be clearly identified by a fin clip during behavioral observations (approximately early July) and concluded when interaction rates declined substantially (e.g., likely due to cold water temperatures in mid-October). Two types of dominance experiments were conducted. The first experiment was designed to assess dominance under contest competition, and the second experiment was designed to assess dominance under scramble competition. In both experiments, fish were anesthetized with MS-222 (tricaine methanesulphonate), fork length (FL, mm) and weight (mg) were recorded, the fish were size-matched to the nearest 1 mm (FL), and the adipose fin was either completely excised or slit so that the fin remained intact. The presence or absence of the fin clip allowed us to differentiate the fish during observations. The slit fin was intended to put the unmarked fish under similar handling procedures as the marked fish. Marks were alternated between aquaria and origin to eliminate any behavioral difference due to marking stress. Fish were allowed to recover from the anesthetic and then stocked in aquaria. One hatchery and one wild spring Chinook salmon were placed in each aquarium. Both fish were introduced at the same time to prevent any prior residence advantage (e.g., Metcalfe et al. 2003).

Fish were acclimated in aquaria for 6 days. This acclimation period was determined by comparing behavioral responses and dominance from pairs of fish that were held for different lengths of time during previous experiments (Pearsons et al. 2001). After 6 days, the behavioral responses and dominance did not generally change. In addition, it was possible to measure differences in growth over this length of time. Fish were fed a total of 10 pellets during each acclimation day, except for the first day stocked and the sixth day when fish were not fed so that they would be hungry and interact on the observation day. During 2003, we increased the size of the pellets that were fed to the fish as fish length increased. During 2004, we used small pellets throughout the duration of the experiment to ensure that fish would not become satiated and cease interacting during the experiments. During the acclimation period, fish interacted with one another, and it is likely that dominance was established prior to the seventh day.

After the 6-day acclimation, food acquisition, agonistic interaction, and habitat location was assessed on day 7. An observer recorded observations from behind a blind constructed out of camouflage netting to prevent fish from seeing the observer. The observer distinguished fish origin based on the presence or absence of a fin clip, but the observer did not know which origin had each clip. The number of food items acquired by each fish was recorded. Agonistic interactions were recorded throughout the duration of the observations. We recorded which fish initiated an interaction and whether they dominated. Dominance of an interaction was assigned to the fish that defended a position or removed another fish from a preferred position. Type of interaction was recorded as follows: nip (contact with mouth open), butt (contact with mouth closed), chase (no contact, swimming after another fish for at least one body length), threat (no contact; for example fin flares, opercle flares, swimming side by side), and crowd (no clear threat but physical presence moved the other fish away) (McMichael et al. 1999). After observations were completed, fish were removed from aquaria, anesthetized with MS-222, and FL (mm), weight (mg), and presence or absence of adipose fin was recorded. Growth was calculated by subtracting the length or weight of each fish at the end of the experiment by the length or weight at the beginning of the experiment.

Contest competition

The aquaria were configured to provide one location that was close to a source of underwater food, water flow, and cover. Food pellets, ground into a slurry, were introduced through a tube with running water to alert fish that food was available. Once both fish had keyed into the food source, one food pellet was added at approximately 1 min intervals. The location of each fish was recorded at least once every minute. The location was expressed as which fish, if any, was in an area that was closest to the source of food, flow, and cover. This was generally in the middle of the tank, from 2.5 to 25 cm off the bottom and from the end of the pipe to 30 cm downflow of the pipe. If both fish were in this zone, then the fish closest to the pipe was assessed to be in the most desirable location. The cover was made out of thick wire, black plastic sheeting on the top, and window screen on the side furthest from the observer and was 20 cm long, 16 cm tall, and 16 cm wide. Total observation time for each replicate was approximately 20–25 min (not including the time that the food slurry was introduced). Dominance was attributed to the fish that won at least two of three categories: acquired the most food, dominated the most behavioral contests, and occupied the location closest to the outlet of the pipe the most. If fish did not consume at least 10 pellets together or if fish did not interact with each other, then they were not included in the analysis because dominance could not be reasonably assessed. All fish were size-matched to the same length (mm FL) except in 2003, when 15 replicates differed in size by 1 mm (nine of the wild fish and six of the hatchery fish were bigger, and this difference was less than 2% of the body length of the smaller fish). This size difference is not thought to be influential in behavioral dominance (Abbott et al. 1985).

Scramble competition

Methods for scramble competition were the same as those for contest competition except for the following differences. The configuration of aquaria was the same except that the cover was removed. In addition, food was introduced onto the surface of the water from behind the blind into one of five locations every minute. The locations were the four corners and the center of the aquaria. The order of food presentation into these locations was rotated. Dominance was assigned to the fish that ate the most pellets. In 2003, the fish were the same length in all but 21 of the replicates, and of these 21 replicates they were 1 mm FL different (12 of the wild fish and 9 of the hatchery fish were bigger, and this difference was less than 2% of the body length of the

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smaller fish). All of the fish were the same size at stocking during 2004.

Growth experiment

To determine if there were inherent differences in hatchery and wild fish to grow and thereby influence our assessment of growth in competition trials, we performed a separate growth experiment during 2004. The protocols and aquaria for this experiment were exactly the same as those used in the contest competition experiment except that only one fish was placed into each aquarium. Equal numbers of replicates were completed for both origins of fish. The same number of pellets (10 during acclimation and 20 on day 7) was added to the tank so that growth in the contest competition experiments could be compared with growth without competition. Measurement of growth was done in the same way as described for contest competition experiments.

Analysis

A variety of parametric and nonparametric tests were used to test for differences among comparisons (Sokal and Rohlf 1981). Paired comparisons between total dominance of hatchery and wild fish were made for each replicate using a two-tailed Wilcoxon matched pairs test. This test was a matched comparison of the sums of the percentages of the food acquisition, habitat used, and interactions dominated in contest experiments and percentage of food eaten in scramble experiments. Comparisons of types (e.g., chase, butt, nip) and frequencies of interactions were made with a G test. Aggressiveness (average interactions initiated per minute for all tanks) was compared with a Mann–Whitney U test for hatchery versus wild fish. To determine sources of aggressive differences and to standardize comparisons, (*i*) dominant hatchery versus dominant wild fish and (*ii*) subordinate hatchery versus subordinate wild fish were compared using the same test. Aggressiveness of dominant fish (regardless of origin) was compared with subordinate fish using a Mann–Whitney U test. Paired comparisons of growth in the competition experiments were compared using a two-tailed paired Student's t test. A paired sign test was used to compare whether fish in each replicate that grew the most were also classified as dominant. Comparisons of growth in the single fish growth experiment were made with a two-tailed Student's t test. With the exception of growth and interaction rate data in scramble experiments, data collected during 2003 and 2004 were pooled because differences between years were not significantly different ($P > 0.05$), and increased sample size contributes to increased statistical power. Differences were considered statistically significant if $P \leq 0.05$. Student's t tests and G tests were calculated using Microsoft Excel, and the remainder of tests was calculated using the software program STATISTICA (StatSoft, Inc. 2001).

Results

Contest competition

Dominance was assessed in 229 out of 255 replicates during 2003 and in 276 out of 314 replicates during 2004. A total of 26 replicates in 2003 were eliminated because fish died or were missing (2: 1 hatchery and 1 both hatchery and wild fish), neither fish ate (14), no interactions were observed (7), or at least one fish behaved abnormally (3: all hatchery; e.g., swimming up and down against the side of the aquarium). Thirty-eight replicates in 2004 were eliminated because fish jumped out of tanks (4: all hatchery), fish died or were missing (5: 1 hatchery, 3 wild, 1 unknown), neither fish ate (12), no interactions were observed (5), or at least one fish behaved abnormally (12: 9 hatchery and 3 wild; e.g., swimming up and down against the side of the aquarium). Most of the failed replicates were caused by both fish in the aquarium exhibiting behavior that would not allow us to assess dominance (22 out of 26 in 2003 and 17 out of 38 in 2004). However, hatchery fish were most often the cause of failed replicates when one fish could be identified as the cause of failure.

Overall dominance scores were not significantly different between hatchery (mean ± 1 standard deviation, SD; 141 ± 124) and wild (mean ± 1 SD; 159 ± 124) fish ($P = 0.058$). Food, habitat, and agonism dominance were consistently higher for wild fish (Fig. 1), and 53% of the replicates were dominated by wild fish (Fig. 1). Of the replicates where fish differed by 1 mm, hatchery fish dominated 1 of 5 replicates when it was bigger, and wild fish dominated 5 of 10 replicates when it was bigger. These results indicate that the small differences in size did not influence dominance. The frequencies of different types of interactions used by hatchery and wild fish were not significantly different (G test, $P = 1.000$; Fig. 2). Wild fish initiated a total of 7865 interactions, and hatchery fish initiated a total of 7245 interactions. Wild fish were 8.1% more aggressive than hatchery fish ($P = 0.05$; Fig. 3), and this difference was likely caused by higher aggressiveness of subordinate wild fish (Fig. 3). Significant differences in aggressiveness were not detected between dominant fish of the two origins (Fig. 3). However, dominant fish (regardless of origin) were more aggressive than subordinate fish ($P < 0.0001$; Fig. 3).

Wild fish gained more weight than hatchery fish (2003 and 2004 combined), and this finding was largely due to differences detected in 2004 (Table 1). Significant difference in length growth of hatchery and wild fish were not detected (Table 1). However, dominant fish, regardless of origin, grew significantly more than subordinate fish in both length and weight (Table 1). Both origins of fish gained weight in 2003 and lost weight in 2004 (Table 1).

Scramble competition

Dominance was assessed in 97 out of 112 replicates during 2003 and in 266 out of 296 replicates during 2004. Fifteen replicates in 2003 were eliminated because fish died or were missing (7: 1 hatchery and 6 wild), neither fish ate (4), no interactions were observed (1), or at least one fish behaved abnormally (3: all wild). Thirty replicates in 2004 were eliminated because fish died or were missing (7: 4 hatchery, 2 wild, and 1 both), neither fish ate (17), no interactions were observed (5), or at least one fish behaved abnormally (1 hatchery). Most of the failed replicates were caused by both fish in the aquarium exhibiting behavior that would not allow us to assess dominance (5 out of 15 in 2003 and 23 out of 30 in 2004). However, wild fish were most of-

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Fig. 1. Comparisons of mean (±1 standard deviation) of the food acquisition, habitat occupation, agonism dominance (agonism), and replicates dominated by wild (open bars) and hatchery (solid bars) fish in contest competition experiments.

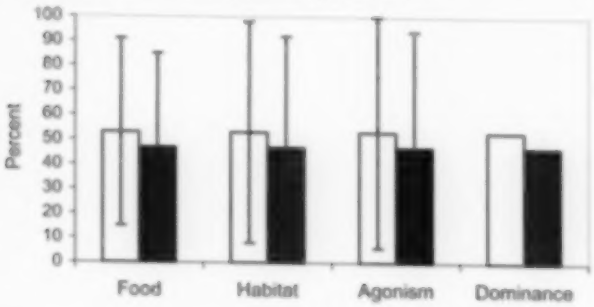
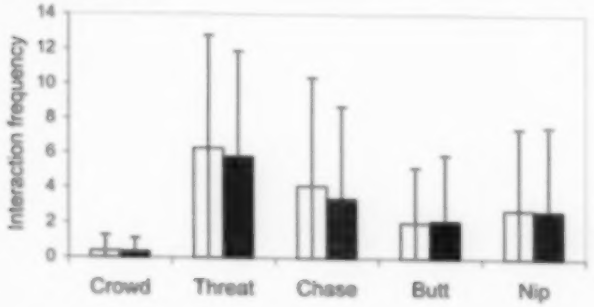


Fig. 2. Comparisons of frequencies of interaction types initiated (mean interaction per fish in each tank ±1 standard deviation) by wild (open bars) and hatchery (solid bars) fish in contest competition experiments.

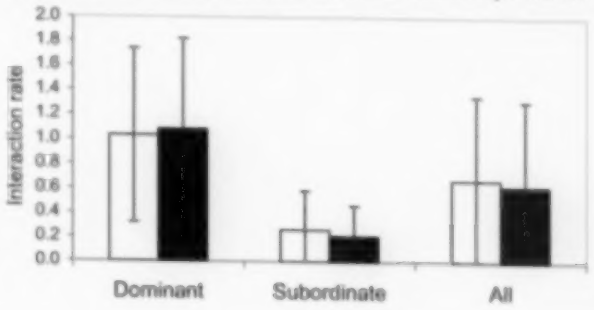


ten the cause of failed replicates when one fish could be identified as the cause of failure.

Overall dominance was not significantly different between hatchery and wild fish ($P = 0.74$); hatchery fish were dominant for 47% of replicates, and dominance was equal in 5% of the replicates (Fig. 4). If the percentage of replicates that were tied for dominance were equally apportioned to origin (e.g., 2.5%), then 49.5% of replicates were dominated by hatchery fish. Food and agonism dominance were slightly higher for wild fish (Fig. 4). Of the replicates where fish differed by 1 mm, hatchery fish dominated 5 of 11 replicates when it was bigger, and wild fish dominated 6 of 10 replicates when it was bigger. These results indicate that the small differences in size did not influence dominance. The frequencies of different types of interactions that hatchery and wild fish used were not significantly different ($P = 1.000$; Fig. 5). Wild fish initiated a total of 6222 interactions, and hatchery fish initiated a total of 5717 interactions. Wild fish were 10.1% more aggressive than hatchery fish (Table 2), and this difference was likely caused by higher aggressiveness of subordinate wild fish than subordinate hatchery fish in 2003 (Table 2). Significant differences in aggressiveness were not detected between dominant fish of the two origins (Table 2). However, dominant fish were more aggressive than subordinate fish ($P < 0.0001$; Table 2).

Hatchery fish lost less weight and grew longer than wild fish (2003 and 2004 combined), and this finding was

Fig. 3. Interaction rates (mean interaction per fish per minute ±1 standard deviation) of agonistic interactions initiated by wild (open bars) and hatchery (solid bars) fish in contest experiments.



largely due to differences detected in 2003 (Table 3). Dominant fish, regardless of origin, grew significantly more than subordinate fish in both length and weight (Table 3). Both origins of fish gained weight in 2003 and lost weight in 2004 (Table 3).

Growth experiment

Growth of single fish was assessed in 125 wild and 125 hatchery origin replicates out of 320. Seventy replicates were eliminated because three fish jumped out of tanks (2 hatchery and 1 wild), and 67 fish ate fewer than 10 pellets on the seventh day (33 hatchery and 34 wild). The same number of hatchery and wild origin fish were responsible for failed replicates (35). There was no detectable difference in growth between wild and hatchery fish ($P = 0.95$; Fig. 6). Mean growth of hatchery and wild fish was considerably higher in single fish replicates than growth of individual fish of the same origin in paired contest experiments during 2004 ($P < 0.0001$).

Discussion

If we had the resources to perform a higher number of replicates in contest competition trials, it is possible that the increased statistical power would have resulted in a significant probability of rejecting the total dominance null hypothesis ($P \leq 0.05$), but the magnitude of difference would still be small. As it was, we had a 5.8% chance of rejecting the null hypothesis of no difference between fish origins in contest competition dominance when it was actually true. Approximately 29 additional replicates would be necessary to detect a significant difference in dominance ($P = 0.050$) if we extrapolate the results we observed for the 505 replicates. That being said, the number of replicates that we conducted is the highest that we are aware of for this type of study. Our study demonstrates that large numbers of replicates are necessary to detect statistically significant differences when differences in competitive dominance are small.

It is not uncommon for replicates in these kinds of studies to be discarded because some behaviors make it difficult to assess dominance (e.g., Metcalfe et al. 2003). We discarded about 5% of the replicates in our study, because we could not assess dominance when fish jumped out of tanks or when fish expressed behavior indicative of wanting to leave an aquarium. However, it is possible that 24 of the replicates

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Table 1. Comparisons of mean (±1 standard deviation in parentheses) wild and hatchery fish growth and percentage of replicates that the dominant fish grew more than the subordinate in contest competition experiments.

		Growth		% of dominant fish that grew more	
Origin	n^a	Length (mm)	Weight (mg)	Length	Weight
2003					
Wild	227	0.44 (1.24)	94.70 (279.32)	75	80
Hatchery	227	0.59 (1.33)	57.72 (290.37)	82	80
P^b		0.133	0.223	<<0.001	<<0.001
2004					
Wild	276	0.31 (0.96)	−52.55 (216.57)	69	87
Hatchery	276	0.34 (0.93)	−102.53 (256.63)	75	84
P^b		0.698	0.026	<<0.001	<<0.001
Total					
Wild	503	0.37 (1.09)	14.22 (257.43)	72	84
Hatchery	503	0.46 (1.14)	−30.21 (283.56)	78	82
P^b		0.156	0.017	<<0.001	<<0.001

[a]Number of replicates.
[b]*P* values for statistical tests.

Fig. 4. Comparisons of mean (±1 standard deviation) food acquisition, agonism dominance, and replicates dominated by wild (open bars) and hatchery (solid bars) fish in scramble competition experiments.

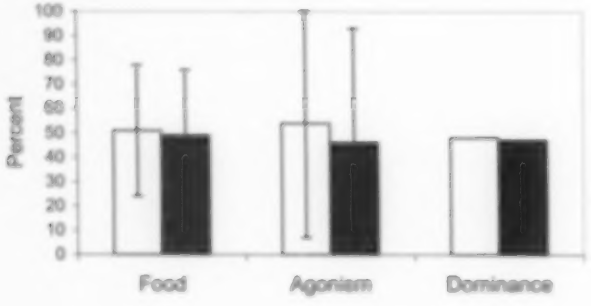
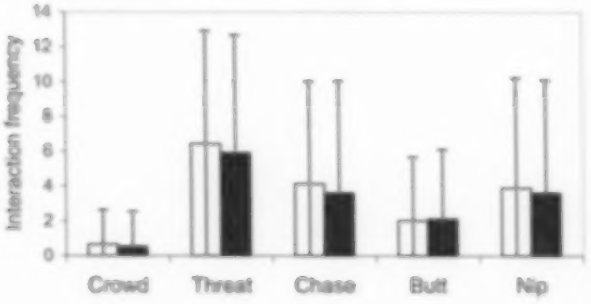


Fig. 5. Comparisons of frequencies of interaction types initiated (mean interaction per fish in each tank ±1 standard deviation) by wild (open bars) and hatchery (solid bars) fish in scramble competition experiments.



that were discarded may have been extreme responses to aggression (e.g., one fish was so aggressive that the other fish tried to leave the aquarium), and in 18 of those, wild fish may have been dominant. If discarded replicates were biased towards wild fish dominance, as is suggested by the data, then it is likely that a significant result would have been observed if dominance could have been quantified. If we assume an average dominance score for these discarded replicates, then a significant difference would be detected (P = 0.041). A significant difference would be consistent with a comparable study conducted during 2002 that used similar fish and facilities in the upper Yakima River Watershed. In that study, wild fish were more dominant than hatchery fish in contest competition experiments (Farrell 2003).

The most important finding of this study is that state-of-the-art fish culture practices, which are intended to minimize domestication selection on competitive dominance, produced effects that were small or undetectable after one generation of hatchery exposure. Although no comparisons were significantly different, wild fish were 6% more dominant in contest experiments and were nearly identical in scramble experiments. In addition, the types and frequencies of agonistic behaviors that were observed between hatchery and wild fish were not significantly different in either contest or scramble experiments. These findings suggest that hatchery fish behaved in a similar manner as wild fish.

It is possible that the behaviors of the two test groups that we observed in our experiments were influenced by selective survival or previous experience, as they were held in circular tanks prior to experimentation. These issues are common to almost all common garden experiments, because test subjects are held or tested in similar environments that may not be identical to natural environments. Selective survival was unlikely in our study because the mortality rates in our tanks were low and represented a small proportion of the experimental population (e.g., <2%). Previous experience is more difficult to rule out. However, there are a number of issues that suggest that it was not a major factor influencing our conclusions. For instance, there was no noticeable differ-

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Table 2. Interaction rates (mean interaction per fish per minute ±1 standard deviation) of agonistic interactions initiated by hatchery and wild fish in scramble experiments.

Origin	n^a	Interaction rate	P^b
2003			
Wild	97	0.60 (0.65)	0.02
Hatchery	97	0.46 (0.66)	
Wild dominant	44	0.61 (0.46)	0.43
Hatchery dominant	46	0.60 (0.68)	
Wild subordinate	46	0.57 (0.72)	0.01
Hatchery subordinate	44	0.27 (0.56)	
2004			
Wild	266	0.82 (0.83)	0.13
Hatchery	266	0.78 (0.91)	
Wild dominant	132	1.17 (0.83)	0.40
Hatchery dominant	123	1.16 (1.01)	
Wild subordinate	123	0.43 (0.61)	0.21
Hatchery subordinate	132	0.35 (0.50)	
Total			
Wild	363	0.76 (0.79)	0.01
Hatchery	363	0.69 (0.87)	
Wild dominant	176	1.03 (0.79)	0.23
Hatchery dominant	169	1.01 (0.96)	
Wild subordinate	169	0.47 (0.65)	0.01
Hatchery subordinate	176	0.33 (0.51)	

[a]Number of replicates.
[b]*P* values from Mann–Whitney *U* tests are for comparisons between hatchery and wild fish regardless of dominance, when they were dominant, and when they were subordinate.

Table 3. Comparisons of mean (±1 standard deviation in parentheses) wild and hatchery fish growth and percentage of replicates that the dominant fish grew more than the subordinate in scramble competition experiments.

		Growth		% of dominant fish that grew more	
Origin	n^a	Length (mm)	Weight (mg)	Length	Weight
2003					
Wild	97	0.37 (0.86)	48.85 (513.12)	39%	48%
Hatchery	97	0.77 (0.80)	285.35 (456.74)	80%	78%
P^b		0.0008	0.0009	0.049	0.015
2004					
Wild	266	0.24 (1.27)	−133.54 (303.66)	68%	80%
Hatchery	266	0.27 (1.11)	−131.06 (294.81)	66%	79%
P^b		0.647	0.937	<<0.001	<<0.001
Total					
Wild	363	0.27 (1.18)	−84.53 (379.64)	61%	72%
Hatchery	363	0.41 (1.06)	−19.79 (391.14)	70%	79%
P^b		0.048	0.015	<<0.001	<<0.001

[a]Number of replicates.
[b]*P* values for statistical tests.

ences in behavior between hatchery and wild fish in circular tanks throughout their rearing or during the months that experimental trials were conducted in aquaria (similar to Salonen and Peuhkuri 2004); behaviors that were exhibited during trials were similar to what we observe among wild fish in the Yakima River (T.N. Pearsons, unpublished data); behaviors used by older, wild fish collected from the river were similar to ones we observed in this study (T.N. Pearsons, unpublished data); and we tested fish under different conditions than how they were reared.

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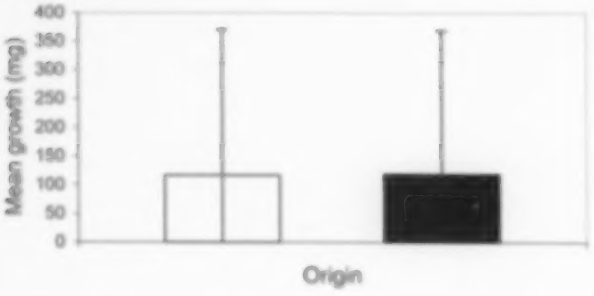
Fig. 6. Comparisons of mean weekly growth (±1 standard deviation) between wild (open bars) and hatchery (solid bars) fish that were reared in isolation.



The behaviors that we observed on the seventh day of our experiment may have been more related to dominance maintenance than establishment of dominance. Fish had the opportunity to interact with each other during the 6 days prior to our observations on the seventh day. Indeed, we saw fish interacting with each other during the days of acclimation as they were being fed. Even though we observed thousands of interactions on the seventh day, the interaction rate and frequency of physical contact behaviors may have been higher during some of the earlier days as fish were trying to establish dominance. In short, the observations that we observed on the seventh day were likely influenced by interactions that had occurred during the previous 6 days and thus were probably better indicators of sustained dominance than if we had used a shorter acclimation time.

Even though our dominance results were not significantly different, wild fish grew (weight) more than hatchery fish in contest experiments, and hatchery fish grew more than wild fish in scramble experiments. This finding supported our original hypothesis that previous rearing environments and selective pressures would influence dominance and produce opposite outcomes. It is possible that our measures of competitive dominance were not as sensitive as our measures of growth. For example, growth was measured during 7 days, but our measure of dominance was measured during approximately 20 min on the seventh day. Ultimately, competitive dominance is probably best measured as a fitness-related trait such as growth than through other habitat and behavioral measures. However, if domestication affects inherent growth rates (Weber and Fausch 2003), then differences in growth rates may not indicate a difference in competitive dominance. For this reason, we have relied primarily on behavioral measures to assess dominance. However, we did not find any difference in growth between the wild and hatchery fish in 2004 when they were reared for 1 week in isolation using the same aquaria and feeding methods as were used in the contest competition experiments. Thus, the differences in growth that we observed were likely due to domesticating effects of competitive dominance.

Fish gained weight in 2003 but lost weight in 2004 during contest and scramble competition experiments. The weight loss in 2004 was likely due to feeding the fish the same weight of food throughout the duration of the experiment. At the same time, the size of fish used in the experiment increased and the water temperature increased. Both of these factors contribute to an increased metabolic demand. In contrast, in 2003 we increased the pellet size (greater mass of food) fed to the fish as fish size and the metabolic demand increased.

Wild fish were significantly more aggressive than hatchery fish in both the contest and scramble experiments. This was largely due to a difference in the aggressiveness of subordinate fish of each origin (i.e., the fish that were dominated). We did not detect significant differences in aggression between dominant fish in either experiment. In other words, wild fish were more likely than hatchery fish to be aggressive towards dominant fish. It is possible that wild fish are more likely to fight for a habitat than hatchery fish, even if a wild fish is not dominant. This may be because energetically profitable locations in natural environments are so heterogeneous compared with hatchery environments and thus worth fighting for (e.g., places are important). In another study, prior residence was found to be more important to wild origin Atlantic salmon than to domesticated Atlantic salmon in determining dominance (Metcalfe et al. 2003). Alternatively, the hatchery origin fish that we tested may not have been very aggressive, because the juvenile life stage of the parents were reared at relatively low densities in the hatchery and had high access to food (Ruzzante 1994). Berejikian et al. (1996) also found that size-matched fry of wild steelhead were initially more aggressive and dominant than those that had been domesticated.

The differences in growth and aggression that we observed were likely due to genetic changes that occurred from one generation of fish culture. However, we cannot exclude the possibility that changes were caused by a maternal rearing environment effect (e.g., not a genetic effect). This might occur if hatchery rearing caused phenotypic differences in females that were passed on to progeny. We believe that this was unlikely to have had much of an effect on our experiments because (*i*) egg sizes of hatchery and wild fish were not significantly different (Knudsen 2005), and (*ii*) fish were tested approximately 4 months after hatching. Most studies that have reported maternal effects in fish have documented relationships between female size and progeny size (Heath and Blouw 1998). We attempted to control for size effects by size-matching our fish. Maternal effects are more likely to occur when fish are very young. In a review of maternal effects in fish, Heath and Blouw (1998) concluded that "maternal effects in fishes are usually negligible beyond the early juvenile life stages".

In comparison with our observations, juvenile coho salmon (Swain and Riddell 1990; Berejikian et al. 1999) and juvenile Chinook salmon (Wessel et al. 2006) reared in hatcheries have been documented to be more aggressive than wild fish, or for steelhead fry, less aggressive (Berejikian et al. 1996). Furthermore, Einum and Fleming's (2001) meta-analysis of aggression revealed that hatchery fish were more aggressive than wild fish. We suspect that the differences in findings are caused by (*i*) the duration and type of hatchery practices and (*ii*) differences in the rearing environment or stock of the fish tested. Most, if not all, of the studies that have previously been conducted have used hatchery fish that have been under culture for more than one generation, and frequently these are of nonlocal origin. If genetic changes or maternal effects are additive, then it is likely that

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larger differences in aggression will be detected with each additional generation of fish culture. Furthermore, fish that are collected from natural environments and compared with fish reared in hatchery environments are likely to produce differences because of the differences in rearing conditions. For example, in another contest competition study, we found that spring Chinook smolts reared in the hatchery dominated salmon smolts that were reared in the Yakima River. Larger fish generally dominated smaller fish, but the size difference did not have to be as great for hatchery fish to dominate as for wild fish (T.N. Pearsons, unpublished data). In short, hatchery fish were dominant over wild fish in contest competition experiments unless wild fish were sufficiently larger than hatchery fish. In a study of coho salmon, Rhodes and Quinn (1998) reported similar findings. It is important to note that competitive dominance does not always result in improved survival. For example, hatchery fish could be competitively dominant at one life stage and still suffer higher rates of mortality because of increased susceptibility to predators, inefficient use of resources, or subordination during another life stage (Bachman 1984; McMichael et al. 1999; Weber and Fausch 2003).

The little (or no) difference in domesticating effects on competitive dominance that was observed in this study was also observed in a sister study examining domesticating effects on vulnerability to predators. Fritts et al. (2007) documented that offspring of hatchery parents were eaten by rainbow trout (*Oncorhynchus mykiss*) and torrent sculpin (*Cottus rhotheus*) predators at a 2% greater rate than offspring of wild parents. The fish used in these predation experiments were from the same matings and same rearing procedures used in this study. Although this difference was significantly different, the size of the difference was very small.

This study and Fritts et al. (2007) support the concept that conservation hatcheries have the potential to produce small domesticating effects after one generation of fish culture. Our results are also consistent with a recent study showing that steelhead from a supplementation hatchery (local origin and single generation hatchery exposure) had reproductive success (adult to adult survival) in natural environments indistinguishable from that of wild steelhead (Araki et al. 2007). There are still considerable scientific uncertainties about the domesticating influence of hatcheries on fish. For example, we do not know whether multiple generations of hatchery culture will produce additive effects or whether cycling through the natural environment will remove any behavioral deficits if they exist. The Yakima/Klickitat Fisheries Project is attempting to answer these questions through a long-term field and laboratory study of domestication. Other field studies will also be necessary before the domesticating influences of behavioral changes can be evaluated within the context of productivity and long-term fitness.

Acknowledgements

We thank the many people who assisted with the rearing of the fish, construction of behavioral arenas, and making behavioral observations. Charlie Strom and his staff at the Cle Elum Supplementation and Research Facility spawned the adults and incubated the eggs. Germaine Hart, Natalia Pitts, Keith Pitts, Bryan Johnson, Timothy Webster, Charity Davidson, and Michael Hamlin helped construct the behavioral arenas and (or) made behavioral observations. Craig Busack, Steve Schroder, Curt Knudsen, and Dave Fast were instrumental in the design of the domestication experimentation in the Yakima Basin. Charity Davidson assisted in arena maintenance and provided office support for the project. Barry Berejikian provided helpful comments on an early draft of the manuscript, and two anonymous reviewers provided comments that improved the manuscript. David Byrnes and Patty Smith provided administrative support of the project. We thank the Bonneville Power Administration for funding this work as part of the Yakima/Klickitat Fisheries Project.

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The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (*Oncorhynchus tshawytscha*) to predation

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Abstract: We tested whether one generation of state-of-the-art hatchery culture influenced the vulnerability of Chinook salmon (*Oncorhynchus tshawytscha*) fry to predators. Size-matched hatchery and wild origin spring Chinook salmon fry were exposed to rainbow trout (*Oncorhynchus mykiss*) and torrent sculpin (*Cottus rhotheus*) predators in 10.8 m^3 net pens. The hatchery origin fry were the offspring of first generation hatchery-reared broodstock, and the wild origin fry had no history of hatchery culture; both originated from the same stock. Wild origin fry were found to have a 2.2% ($p = 0.016$) survival advantage over hatchery origin fry during 2 years of predation challenges. The most important findings of this study are (*i*) domestication can affect the susceptibility to predators after only one generation of state-of-the-art hatchery culture practices, and (*ii*) the domestication effect was very small.

Résumé : Nous vérifions si un élevage pendant une génération dans une pisciculture de pointe influence la vulnérabilité des alevins de saumon chinook (*Oncorhynchus tshawytscha*) aux prédateurs. Nous avons exposé des alevins de saumons chinook du printemps, de pisciculture et d'origine sauvage, appariés en fonction de la taille, à des prédateurs, des truites arc-en-ciel (*Oncorhynchus mykiss*) et des chabots de torrent (*Cottus rhotheus*), dans des enclos de filet de 10,8 m^3. Les alevins de pisciculture étaient les rejetons d'un stock reproducteur de première génération d'élevage en pisciculture et les alevins sauvages n'avaient aucun antécédent d'élevage en pisciculture; les deux groupes provenaient d'un même stock. Les alevins d'origine sauvage ont eu un avantage de survie de 2,2 % ($p = 0,016$) sur les alevins d'élevage au cours des deux années de confrontation avec les prédateurs. Les résultats les plus importants de notre recherche sont que (*i*) la domestication affecte la vulnérabilité aux prédateurs après une seule génération d'élevage dans des conditions de pisciculture de pointe et (*ii*) l'effet de la domestication est très petit.

[Traduit par la Rédaction]

Introduction

Propagation of fish in hatcheries has the potential to unintentionally change the genetic composition of donor populations and subsequently contribute to reduced survival in natural environments. This is a particular concern for supplementation or conservation hatcheries because the objective of these hatcheries is to increase natural production (Mobrand et al. 2005). The mechanism of genetic change most likely to occur in conservation hatcheries is domestication (i.e., natural selection in artificial environments; Busack and Currens 1995; Campton 1995). Conservation hatcheries use methods such as representative broodstock selection, factorial mating, low rearing densities, and a high proportion of natural origin fish in the broodstock to control for other sources of potential genetic change (Busack and Currens 1995).

Domestication selection may be most extreme when ecological conditions such as predation are dramatically different between natural and hatchery environments. Natural environments contain a diversity of predators such as sculpins (*Cottus* spp.) (Ricker 1941; Hunter 1959) and rainbow trout (*Oncorhynchus mykiss*) (Beauchamp 1995), and the mortality of young salmonids caused by predation can be substantial (Fresh and Schroder 1987; Rieman et al. 1991; Ruggerone and Rogers 1992). In contrast, predators, particularly fishes, are generally absent from the rearing environments of conservation hatcheries (Maynard et al. 1995). The relaxation of predator-induced mortality in hatcheries can result in the survival of genotypes that would be selected against in natural environments. This can result in genetic differences that are maladaptive in natural environments and ultimately result in reduced survival.

Various laboratory studies have demonstrated differences in predation mortality or predator avoidance behavior between hatchery and wild fish. Genetic differences between hatchery and wild origin steelhead trout (i.e., sea-run *O. mykiss*) increased the predation mortality of hatchery origin fish when exposed to a benthic predator (Berejikian 1995). Other researchers have found behavioral evidence

Received 10 April 2006. Accepted 5 March 2007.
Published on the NRC Research Press Web site at cjfas.nrc.ca on 14 June 2007.
J19267

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 doi:10.1139/F07-057 © 2007 NRC Canada

that hatchery origin steelhead trout and brown trout (*Salmo trutta*) were more vulnerable to predation than their wild origin counterparts (Johnsson and Abrahams 1991; Fernö and Järvi 1998; Álvarez and Nicieza 2003). Of the aforementioned studies, only Álvarez and Nicieza (2003) tested predation vulnerability after a single generation of hatchery rearing, and only Fernö and Järvi (1998) and Berejikian (1995) used fish that were from the same donor stock. It is important to test fish after limited exposure to hatchery environments because that is one of the strategies used in conservation hatcheries (at least one generation of natural spawning between hatchery culture) to limit domestication. Furthermore, using the same stock is important because genetic differences between stocks can confound results. In addition, none tested for direct evidence (actual consumption) of vulnerability using both a benthic and a midwater predator, both of which are potential predators to young salmonids. Sculpins are generally ambush type predators that live on the stream bottom and blend in with their surroundings, while trout are generally a cruising type predator that are more visible and tend to overtake their prey in short bursts of speed. Prey fish may use different tactics to avoid capture by predators with different foraging methods so it is important to challenge fish with different predators. Finally, none used yearling Chinook salmon (*Oncorhynchus tshawytscha*) as the prey species.

The purpose of this study was to determine if there are inherent differences in the survival of wild origin and first generation hatchery origin spring Chinook salmon fry when exposed to predators. We conducted a common garden experiment to control for nongenetic factors that could influence survival. These fry were produced at a state-of-the-art supplementation facility that is the centerpiece of the Yakima/Klickitat Fisheries Project (YKFP) to increase natural production of Chinook salmon.

Materials and methods

This work was conducted on stream-type (Healey 1983) spring Chinook salmon fry in the upper Yakima River in central Washington State, USA. The wild origin (hereafter termed wild) fry used in our study are the offspring of wild, naturally spawned spring Chinook salmon. The hatchery origin (hereafter termed hatchery) fry are the offspring of returning first generation hatchery-reared adults, which were derived from the same stock (population) as the wild adults. The adult broodstock were collected downstream of the spawning grounds at Roza Dam throughout the duration of the spring migration so that a representative sample of the population in terms of return timing, age, and size were obtained (Knudsen et al. 2006). Adult broodstock were held in a concrete raceway at the hatchery until spawning commenced in early September. For a detailed description of the supplementation program, see Knudsen et al. (2006).

During spawning, gametes were collected and fertilized according to a standard mating protocol of 3 × 3 factorial crosses to maintain genetic diversity. A sample of fertilized eggs (mean 199; range 169–275) from each parental cross were placed in individual incubation containers (10.2 cm diameter × 5 cm tall isolettes) and incubated in Heath trays (Knudsen et al. 2005). To obtain the experimental fry, we randomly selected isolettes until nearly all of the adult broodstock used for the factorial crosses were represented at least once and we had enough fry to conduct our study. All surviving fish in the selected isolettes were used. This ensured that our sample of experimental fish represented the true reproductive effort expressed by each parental cross. During 2003, we selected approximately 12 000 fry of each origin: hatchery-by-hatchery parents (hatchery line) and wild-by-wild parents (wild line). This represented the progeny of 33 wild females, 25 wild males, 32 hatchery females, and 15 hatchery males. This accounted for 58 wild families and 59 hatchery families. During 2004, we selected approximately 8000 fry of each origin. This represented the progeny of 18 wild females, 18 wild males, 20 hatchery females, and 20 hatchery males. This accounted for 54 wild families and 58 hatchery families. These fish were transferred outside into two identical 1710 L polyethylene, conical-bottomed circular tanks on 17 April 2003 and 19 April 2004 as unfed fry.

Predation trials were conducted in a 3 m × 30 m concrete raceway at the Cle Elum Supplementation and Research Facility in Cle Elum, Washington. Eight 3 mm nylon mesh net pens measuring 3 m long × 2.4 m wide × 1.5 m high were placed in the raceway to contain each group of trials. Net pens were totally enclosed with a zippered top. Each net pen included one 0.8 m and one 1.3 m diameter floating hoop covered with black plastic to provide overhead cover and a 1.2 m tall plastic evergreen tree to provide in-water cover.

Predators were collected by backpack electrofishing and angling in nearby Yakima Basin streams and were introduced into the net pens at least 1 day prior to the introduction of the fry. Each net pen received three rainbow trout and three torrent sculpin (*Cottus rhotheus*) during 2003. Two rainbow trout and two torrent sculpin were used per pen during 2004 to reduce the fry mortality to less than 50% and avoid density-dependent selection of the predators (i.e., switching to the consumption of less vulnerable prey as the more vulnerable individuals become scarce). Using fewer predators also made it easier to collect enough replacements for the predator assemblages periodically throughout the experiment to avoid the possibility of pseudoreplication (Hurlbert 1984). We therefore used a new assemblage of predators for every other week of trials during 2004 (Table 1), but used the same assemblage of predators throughout 2003 (Table 1).

Trials were conducted between 19 May and 23 June 2003 and between 3 May and 28 June 2004 (Table 1). Each weekly trial started on Monday with the introduction of 100 hatchery and 100 wild, size-matched fry. Before introduction into the net pens, all fry were anesthetized in a solution of tricaine methanesulfonate, measured to the nearest millimetre fork length (mm FL), and differentially marked by excising a small amount of fin tissue from the tip of either the upper caudal or lower caudal. These marks were alternated between net pens and origins to eliminate any possible introduced biases between clip types. A subsample (753 hatchery and 753 wild) was also weighed to the nearest milligram to compare the condition of the fry. All data was entered directly onto a microcomputer, and the mean lengths of the two stocks of fry were matched as closely as possible. The

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Table 1. Dates the trials were performed, the predator sets used, and the mean (ranges in parentheses) fork lengths of rainbow trout (*Oncorhynchus mykiss*) (RBT) and total lengths of torrent sculpin (*Cottus rhotheus*) (TSC) at the time of stocking during 2003 and 2004.

Date fry stocked	Week no.	Predator set	RBT (mm)	TSC (mm)
19 May 2003	1	1	204.4 (178–252)	112.1 (92–143)
26 May 2003	2	1	—	—
9 June 2003	3	1	—	—
16 June 2003	4	1	—	—
3 May 2004	1	1	185.2 (161–229)	108.3 (95–124)
10 May 2004	2	1	—	—
24 May 2004	3	2	172.2 (161–204)	114.4 (103–141)
31 May 2004	4	2	—	—
7 June 2004	5	3	171.4 (153–209)	113.3 (96.5–134.5)
14 June 2004	6	3	—	—
21 June 2004	7	4	189.6 (150–249)	113.25 (102–133)

Note: A predator set is a group of three (2003) or two (2004) rainbow trout and three (2003) or two (2004) torrent sculpin.

fry were then allowed to recover from the anesthetic before being introduced simultaneously into the net pens. Food for the fry was introduced into each net pen from Tuesday through Thursday to ensure that weakening due to hunger did not influence survival. Feeding also introduced a situation where the fry had to choose whether to increase their exposure to predation to feed. Each weekly trial was terminated on Friday, when all surviving prey were removed, enumerated, measured to the nearest mm FL, and interrogated for marks to assign origin. Nets were also examined for the presence of dead fry. We assumed that all missing fry were consumed and did not die from causes other than predation. To evaluate this assumption, we gastrically lavaged the predators (Light et al. 1983) at the end of week 6 in 2004 and enumerated the number of fry contained in each predator by counting whole fish and paired diagnostic bones from partially digested fish (Hansel et al. 1988). We also compared the mortality of the two origins of fry in the circular holding tanks to determine if one origin was more likely to die in the absence of predators.

We used analysis of variance (ANOVA) to test whether the sizes of the predators used were similar between net pens. Two-tailed Student's t tests were used to test for differences in the mean lengths of the two stocks in each net pen. In addition to the t tests for the means, we used the G test of independence, with the null hypothesis that the sizes of fry had the same distribution at stocking. The length–weight relationships of the fry at stocking were compared using analysis of covariance (ANCOVA), with log-transformed weight as the dependent variable and log-transformed length as the covariate. To determine if replicates performed with the same predator assemblages were independent, we compared the differences in survival between the two origins of fry for each net pen replicate in the first exposure to a predator assemblage with the survival differences in subsequent exposures to those predators using the Pearson's correlation coefficient. If there were dependency among the predators, we expected to find a correlation that would indicate that subsequent exposures could not be used as true individual replicates. The 2003 and 2004 differences in survival of the two origins for each replicate were tested using the Mann–Whitney U test. If no significant difference were found, it would indicate that it is appropriate to pool the 2 years of data. Wilcoxon matched pairs tests were used to test whether there were differences in survival between the two stock origins. The ANOVA and Student's t tests were calculated using Microsoft Excel, and all other tests were calculated using STATISTICA software (StatSoft, Inc. 2001). All tests were considered significant at $p < 0.05$.

Results

The mean lengths of the predators in all net pens were similar (Table 1), and the lengths of predators in each net pen did not differ significantly (ANOVA; $F = 0.125$, df = 39, $p = 1.0$). We found no significant differences between the mean fork lengths (t test, $p > 0.05$) of the hatchery and wild fry that were introduced into the net pens. The size distributions of the hatchery and wild fry at introduction differed significantly in 4 of the 84 replicates (G test, $p < 0.05$). The mean fork lengths of the two origins of fish at introduction never varied by more than 0.4 mm within a net pen trial. The condition (length–weight relationships) of the fry were the same at the time of stocking (ANCOVA; $F = 0.5$, df = 1, $p = 0.48$).

If a specific assemblage of predators in a net pen were prone to keying in on a certain physical or behavioral trait of one of the two origins of fry, then reusing that assemblage of predators would not constitute a true replicate and would skew the results. Using the Pearson's correlation coefficient, we found no indication of dependency among the predators between the first and second exposure ($r = 0.273$, df = 30, $p = 0.13$), the first and third exposure ($r = 0.263$, df = 6, $p = 0.53$), or the first and fourth exposure ($r = -0.506$, df = 2, $p = 0.49$). There was also no difference in the survival differences between years (Mann–Whitney U, $p = 0.54$). We therefore combined all trials during 2003 and 2004 to perform Wilcoxon matched pairs tests to increase the statistical power of our tests.

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Virtually all of the mortalities were consumed fish. Only four hatchery fry and three wild fry out of 8400 stocked per origin were recovered as uningested mortalities. There was no evidence these mortalities were caused by predation, so they were not included as such in the statistical tests. We were able to recover direct evidence of 37% of the fry that were missing during week 6 of 2004 via gastric lavage. The remaining fry may have been completely digested if they were consumed within the first 2 or 3 days of a trial (Elliot 1991). It is also unlikely that the fry died from other causes before being eaten because the mortality of the fry in the circular holding tanks throughout the duration of our study was very low (<1%).

For all 84 trials combined, hatchery fry survival averaged 69.0% (standard deviation, SD = 18.68), and wild fry survival averaged 71.2% (SD = 17.31). Hatchery fry survival was higher in 32 of the trials, wild fry survival was higher in 46 of the trials, and survival was equal in six of the trials. We found significantly higher survival of the wild fish over the hatchery fish for both years combined using all of the predator exposures ($Z = 2.42$, $n = 84$, $p = 0.016$). We also tested only the first exposures, as a more conservative test, which resulted in the same conclusion as the pooled test ($Z = 1.98$, $n = 40$, $p = 0.047$).

Discussion

The data indicate that domestication can affect predation vulnerability in spring Chinook salmon populations after only one generation of state-of-the-art hatchery culture. The hatchery fish used in our study were cultured using practices typical of conservation hatcheries such as collecting broodstock that are representative of the wild population, random mating to avoid conscious or unconscious selection for certain traits, mating using factorial crosses to increase genetic diversity, and their parents were reared at low densities as juveniles (Busack and Currens 1995; Fast 2002). We know of no other studies that tested predation survival differences after only one generation of hatchery culture. Other studies that have found survival or behavioral differences between cultured salmonids and wild salmonids used fish that were artificially cultured for more than one generation (Vincent 1960; Berejikian 1995; Fernö and Järvi 1998) or under intentional selection for traits such as faster growth for farming operations (Johnsson and Abrahams 1991; Fleming and Einum 1997; Yamamoto and Reinhardt 2003). The only study of predation and domestication during the early stages of hatchery culture that we know of (Álvarez and Nicieza 2003) tested behavioral responses to a predator rather than directly testing survival.

Even though we detected a difference in survival after only one generation of hatchery culture, the difference was very small. The hatchery fry used in our study were only 2.2% more vulnerable to predation than the wild fry. In a companion study using the same Chinook salmon populations, Pearsons et al. (2007) observed a small difference in competitive dominance, although the difference was not statistically significant. Other studies have reported larger differences in survival. For example, Berejikian (1995) found nearly a 12% difference in survival between hatchery and wild origin steelhead fry. It is likely that the bigger differences in survival were due to length of hatchery culture (one to seven generations) and fish culture practices. Hatcheries that continually use returning hatchery-reared fish as broodstock can compound the effects of domestication over generations because the genetic traits that lead to higher vulnerability to predators will not be selected against in the protected hatchery environments. Undergoing at least one generation of natural selection in the natural river environment between hatchery culture is theorized to reduce domesticating effects (Busack and Currens 1995) in hatchery fish. Unfortunately, few empirical data exist to examine this phenomenon.

We attempted to control for nongenetic differences in predation vulnerability, such as fish size, condition, and handling, by ensuring our fish were size-matched within a net pen and received the same amount and type of handling. Smaller fish may not be able to evade predators as well as larger fish because they are not able to swim as fast (Taylor and McPhail 1985). Studies have shown that smaller salmonids are more vulnerable to predators than larger salmonids (Patten 1977; Hargreaves and LeBrasseur 1986; Fritts and Pearsons 2004). Because our fish were size-matched and the condition (fatness) of the fish was the same, this would not explain the survival difference that we observed. The sizes of the predators in each net pen were also similar, which reduces the possibility of size-selective predation. Alternating the marks between upper and lower caudal fins ensured that both origins of fry were treated equally. Mortality in the circular tanks holding the experimental fry during the period of the predation trials was very low (0.88% hatchery and 0.87% wild), suggesting that differential mortality from sources other than predation could not explain the differences we observed. In addition, size-matching the fry made it less likely that environmentally based maternal effects (Heath and Blouw 1998) could have caused the difference that we observed. Furthermore, our tests were conducted at least 1 month after the fry began feeding. Heath and Blouw (1998) reported that a maternal effect of female body size to offspring size disappeared soon after the fry began feeding.

The cause of the survival difference that we observed is uncertain. A greater proportion of hatchery fish may have exhibited behaviors that made them more conspicuous, attractive, or less wary and less able to elude predators. Because we did not perform rigorous behavioral observations during the trials, we do not have data to adequately explain why the hatchery fish were more vulnerable to predation than wild fish. However, we did observe that the fry generally formed a single-mixed origin school when introduced into the net pens, and no obvious differences in behavior between the two origins were observed. Because the survival difference between the two origins was small, any behavioral differences would probably be small as well. Behavioral differences of this magnitude are very difficult to detect even in a carefully controlled experiment. Pearsons et al. (2007) reported that 534 replicates were necessary to detect a significant difference in competitive dominance experiments between these same two populations because the actual difference was very small after one generation of hatchery culture. Many studies attribute the willingness of fish to risk exposure to predators as an effort to obtain more food (Johnsson and Abrahams 1991; Yamamoto and Reinhardt 2003). Hatchery origin fish are

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sometimes selected for higher growth hormone levels (Fleming et al. 2002) and would therefore need to take more risks to maintain their higher rate of growth. This seems unlikely for our population because Pearsons et al. (2007) performed experimental trials to assess growth using the same two study populations and found no difference in growth.

To control for environmental effects and measure differences caused by genetic divergence, we performed this study entirely in an artificial environment in a common garden setting. This makes it difficult to quantify how the relative differences that we found would manifest in the natural environment on naturally produced fish. When predation is substantial in the natural environment, the genetic difference that we measured will likely contribute to a difference in survival. Although we included in-water and overhead cover, the natural environment is much more complex than our test arena, with a much wider array of cover, such as rocky substrate, woody debris, aquatic macrophytes, shallow margins, and turbidity. This higher complexity of the natural environment could either amplify or mute the relative difference in predation vulnerability that we measured. Even though we do not know how the magnitude of the difference that we measured would manifest in the natural environment, a genetic difference after only one generation of carefully conducted hatchery culture is an important finding that will likely have ramifications to the natural population.

The number of families that we used (over 50-origin^{-1}·year^{-1}) is far greater than other studies of predation and domestication (e.g., 4–11 families). If only a few families were tested, one family with attributes that made them exceptionally good or poor at avoiding predators could have driven the conclusions of the study. Our results are more likely to be reflective of the whole population rather than just the individuals that were tested. Using two kinds of predators also sets our study apart from others. Fry generally formed a single school and swam along the bottom of the net pens during short observations immediately after their introduction to the pens. It was not uncommon to witness two or three predatory attacks by the sculpins during those first 5 min. Upon fry recovery on the last day, fry were generally higher in the water column underneath the overhead cover where the sculpins were not able to attack them. Qualitative examinations of the gut contents revealed that both predator species consumed many fry and that the timing of predation was different between species. The appearance of the sculpin stomach contents indicated that most of their fry consumption occurred early in the experiment, because the fry were mostly in the advanced stages of digestion, while the rainbow trout stomachs included fry in various stages of digestion (from only bones remaining to freshly ingested).

In summary, we found that small changes in predation vulnerability occurred after only one generation of state-of-the-art hatchery culture. It is uncertain what genetic manifestation caused these fish to survive at different rates and what magnitude of impact this will have to offspring of fish that spawn in the natural environment. Additional studies will be required to understand why differences occurred and to evaluate changes compared with a wild control population and a production hatchery population over several generations so that the long-term fitness of the supplemented population can be measured. The goal of the YKFP is to address these issues in the Yakima Basin so they can be applied to supplementation programs in other basins.

Acknowledgements

This work would not be possible without the assistance and coordination of the Yakama Nation Fisheries staff at the Cle Elum Supplementation and Research Facility. Craig Busack, Curt Knudsen, and Steve Schroder were instrumental in the initial design of this experiment. Michael Hamlin, Germaine Hart, Charity Davidson, Bryan Johnson, Christopher Johnson, Keith Pitts, Natalia Pitts, Gabriel Temple, and Timothy Webster all assisted with the implementation and collection of data. Two anonymous reviewers provided comments that improved the presentation of this work. This work was funded by the Bonneville Power Administration (BPA) as part of the YKFP. Special thanks are owed to David Byrnes and Patty Smith of the BPA for helping to administer the funding for this work.

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Compensatory growth in threespine sticklebacks (*Gasterosteus aculeatus*) inhibited by experimental *Schistocephalus* infections

Hazel A. Wright, Robert J. Wootton, and Iain Barber

Abstract: Compensatory growth responses are made by individual fish to restore their original growth trajectory following a period of growth depression. Little is known about whether diseases impact a fish's capacity for growth compensation. In this study we investigate the effect of *Schistocephalus solidus*, a common cestode parasite of threespine sticklebacks (*Gasterosteus aculeatus*), on the ability of host fish to undertake growth compensation following short-term food deprivation. Placebo-infected controls completely compensated for a 2-week deprivation period after 3 weeks postdeprivation feeding, but experimentally infected sticklebacks showed only partial compensation and after 6 weeks of refeeding had attained only 80% of the weight of continually fed infected fish. A major factor limiting the compensatory growth response of infected fish was their reduced hyperphagic response during the period of refeeding. Feed deprivation had no effect on ultimate parasite size of infected fish. We discuss the possible mechanisms limiting hyperphagia in infected fish and consider the fitness implications — for parasites and hosts — of the reduced ability of infected fish to undertake compensatory growth responses.

Résumé : Les réactions de croissance compensatoire servent chez les poissons individuels à rétablir leur trajectoire originale de croissance après un épisode de croissance réduite. On a peu d'information sur l'impact possible de la maladie sur la capacité d'un poisson de faire une croissance compensatoire. Dans notre travail, nous étudions l'effet de *Schistocephalus solidus*, un cestode parasite commun de l'épinoche à trois épines (*Gasterosteus aculeatus*), sur la capacité du poisson hôte de faire une croissance compensatoire après une courte période de privation de nourriture. Les poissons témoins à infection simulée compensent complètement une période de privation de nourriture de 2 semaines après 3 semaines d'alimentation suivant le jeûne; cependant, les épinoches infectées expérimentalement ne font qu'une compensation partielle et, au bout de 6 semaines après la reprise de l'alimentation, n'ont atteint que 80 % de la masse des poissons infectés nourris sans interruption. Une facteur important qui inhibe la réaction compensatrice chez les poissons infectés est la réduction de leur réaction d'hyperphagie durant la période de reprise de l'alimentation. La privation de nourriture n'a aucun effet sur la taille finale des parasites chez les poissons infectés. Nous discutons des mécanismes possibles de limitation de l'hyperphagie chez les poissons infectés et examinons les conséquences sur la fitness — tant chez les parasites que les hôtes — de la capacité réduite des poissons infectés à entreprendre des réactions de croissance compensatoire.

[Traduit par la Rédaction]

Introduction

Parasitic infections potentially interfere with normal patterns of the growth of host fish through a number of mechanisms. Most intuitively, because host-derived energy used by parasites for growth and development is not available to the host, infections with energy-demanding parasites can be associated with reduced host growth (Barber and Svensson 2003; Finley and Forrester 2003). Parasites that have behavioural effects also have the potential to reduce host growth indirectly by altering the competitive foraging success of their hosts (Milinski 1990; Barber and Ruxton 1998). Alternatively, for parasites that castrate their hosts — yet impose only a limited energetic drain on host resources — the release of resources otherwise destined to fuel sexual development may lead to accelerated somatic growth of hosts, potentially leading to host gigantism (Wilson and Denison 1980; Sorensen and Minchella 1998; Arnott et al. 2000).

When parasitic effects on host growth are studied experimentally in the laboratory, hosts are typically held under a carefully controlled, constant feeding regime and ration. This contrasts with the situation in natural environments,

Received 15 September 2006. Accepted 2 March 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 20 June 2007.
J19536

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 doi:10.1139/F07-056 © 2007 NRC Canada

where food resources are temporally variable in quality and quantity. Studying the effects of parasites under unnatural, invariable feeding conditions may overestimate differences in the growth of parasitized and nonparasitized individuals compared with field studies (e.g., Taskinen 1998), or it may mask them. For example, animals with indeterminate growth, such as fish (Wootton 1998), can balance periods of slow growth during food shortages with phases of accelerated, compensatory growth (CG) during subsequent periods of food availability (Wilson and Osborne 1960). If parasites interfere with the mechanism of growth compensation, then laboratory studies of host growth — carried out under constant ration conditions — are likely to underestimate the impacts that parasites have under more natural, variable feeding conditions.

In fishes, CG responses are primarily achieved by increased food intake (hyperphagia) when food becomes available, though changes in metabolism, growth efficiency, or activity may also play a role (Ali et al. 2003). Hyperphagic responses allow previously food-deprived individuals to achieve a cumulative food intake equal to (or even greater than) that of individuals fed continually over the same time period (e.g., Ali and Wootton 1998, 2000). As a consequence, the body sizes of previously food-deprived individuals can converge with (Jobling 1994) or even exceed (Hayward et al. 1997) those of continually fed individuals held under otherwise comparable conditions (Ali et al. 2003). The extent to which individuals vary in their responses to nutritional deficits and in their ability to undertake CG is poorly understood (Metcalfe and Monaghan 2001), but if parasitic infections restrict a host's capacity to substantially elevate normal levels of food intake, then the ability to compensate may be restricted to healthy individuals. Yet, while CG responses are known to vary with ontogeny (Bertram et al. 1993), gender (Toigo et al. 1999), and nutritional status (Broekhuizen et al. 1994), to date no studies have examined the effects of parasites or disease on CG responses in fish. Here, we report the first experimental test of the hypothesis that parasitic infections can influence host growth by impairing the CG responses of hosts, using the threespine stickleback – *Schistocephalus solidus* model system.

The growth of *Schistocephalus solidus* (Cestoda: Pseudophyllidea) plerocercoids imposes a substantial energy drain on threespine sticklebacks (*Gasterosteus aculeatus* L.) (Lester 1971; Pascoe and Mattey 1977). Infections are associated with reduced host growth (Pennycuick 1971), energy reserves (Arme and Owen 1967), and gonad development (e.g., Bagamian et al. 2004) and increased mortality under nutritional stress (Walkey and Meakins 1970). Infections are also associated with altered foraging behaviour (e.g., Milinski 1984; Ranta 1995) and reduced competitive ability (Barber and Ruxton 1998), as well as decreased meal size of host sticklebacks (Cunningham et al. 1994; Wright et al. 2006), suggesting that hyperphagic responses may be impaired. The specific aims of our study were therefore to determine (*i*) whether infection impairs the host's capacity to show CG responses following a period of food deprivation and (*ii*) whether impaired CG could be explained in terms of altered hyperphagia.

Materials and methods

Experimental infections

Young-of-the-year sticklebacks, collected in April 2002 from Llyn Frongoch (a small upland reservoir in mid-Wales, UK; 52°21′41″N, 3°52′46″W, 290 m altitude) were reared to sexual maturity in mixed sex groups in 96 L laboratory aquaria and allowed to spawn naturally. Embryos were transferred to incubators (Barber and Arnott 2000), and the newly hatched fry fed first on infusoria, *Artemia* nauplii, then live whiteworm (*Enchytraeus* sp.) and frozen bloodworm (*Chironomus* sp. larvae) prior to exposure to the parasite. Because the proportion of *S. solidus* successfully establishing in host fish after experimental infection is often low (e.g., Arnott et al. 2000), the size of the *S. solidus*-exposed group was increased relative to the number of placebo-exposed controls, and exposed fish were fed multiple infective parasites. At a size of ~20 mm (~0.15 g), 20 sticklebacks were each fed copepods (*Cyclops strenuus*) containing a total of five infective (i.e., cercomer-bearing; Smyth 1994) *S. solidus* procercoids (see Smyth 1994 and Barber and Svensson 2003 for details of in vitro parasite culture and exposure protocols). Sixteen placebo-exposed control sticklebacks were fed noninfected copepods. All fish used in this study were juveniles, meaning that the proportion of males and females in each group could not be determined until autopsy. Fish were then transferred individually to separate 14 L (350 mm × 220 mm × 200 mm) tanks within a filtered and aerated recirculating system. Water temperature was maintained at 15 ± 0.5 °C and a photoperiod of 12 h light : 12 h dark was used.

Feeding regimes

For 3 weeks, all individually housed fish were provided daily with an excess of preweighed (to 0.001 g) live whiteworm and allowed to feed to satiation. Food was always freely available and at no point during the study did fish consume all the food provided. Uneaten food was collected each day 24 h after feeding, allowing the daily food consumption of individual fish to be calculated. Ten of the fish exposed to *S. solidus* and eight of the noninfected fish were then fed a maintenance ration of 2% body weight per day for 2 weeks, which allowed them to maintain body weight but not grow. The 10 remaining exposed fish and eight uninfected controls were fed to satiation during this period. All fish were then fed to satiation for a further 6 weeks to allow any compensatory response in weight, length, and condition of the previously food-deprived fish to occur. At weekly intervals, each fish was weighed (to 0.001 g) and digitally photographed from above to allow length measurements (to 0.1 mm) to be made using computerised image analysis (Barber and Svensson 2003). Fish were not anaesthetized prior to being weighed because of concerns over behavioural and appetite effects of repeated anaesthesia and the potential for an interaction with infection status.

At the end of the study, all fish were sacrificed, weighed, measured, and dissected to confirm gender and infection status. *Schistocephalus solidus* plerocercoids recovered from the body cavities of infected fish were blotted dry and weighed (to 0.001 g). The liver was removed at autopsy and

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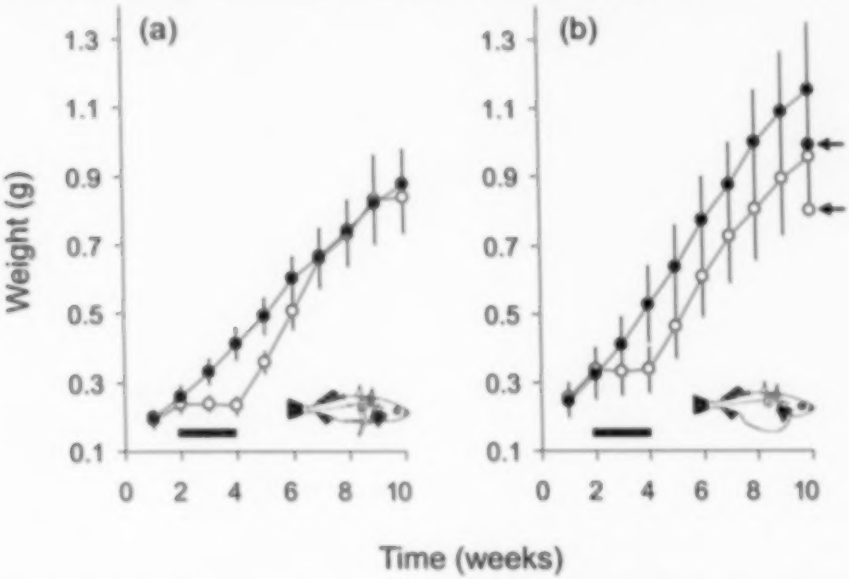
Fig. 1. The growth trajectories of (*a*) noninfected and (*b*) experimentally infected threespine sticklebacks (*Gasterosteus aculeatus*) held under continual feeding conditions (●) or under a compensatory growth regime incorporating a 2-week period of food deprivation denoted by the horizontal bar (○). Data points are means ± standard error. In (*b*), arrows indicate the mean terminal weight of infected fish, minus the parasite weights, receiving either continual feeding (●) or a compensatory regime (○).



weighed separately (to 0.001 g). Fish that were exposed to *S. solidus* but did not develop infections (n = 10) and female fish that released eggs during the study (n = 4, all noninfected) were removed from the analysis. Final group sizes were therefore as follows: infected, deprived regime (ID): n = 5; infected, continually fed regime (IC): n = 5; uninfected, deprived regime (UD): n = 5; uninfected, continually fed regime (UC): n = 7.

Statistical analysis

Initial weights and lengths were compared with two-factor (diet regime, infection status) analysis of variance (ANOVA). Weights at the end of the deprivation period were compared by two-factor analysis of covariance (ANCOVA), using initial weight as the covariate. The trajectories of weight change over the refeeding period were analysed with repeated measures ANOVA. ANCOVA, using initial weight as the covariate, compared the final weights of fish and parasites in each treatment group.

Weight-at-length provides a measure of fish condition. For each week of the refeeding period, two-factor ANCOVA was used to compare weight-at-length across treatments. Liver weight, corrected for body size, also gives an indication of medium-term energy reserves (Chellappa et al. 1995). At the end of the experiment, fish liver weights were analysed by two-factor ANCOVA, with final length as the covariate.

Weekly changes in body weight were expressed as specific growth rate (SGRw). SGRw was calculated as $[(\ln W_f - \ln W_i)/t] \times 100$, where W_f is the final weight (to 0.001 g), W_i is the initial weight (to 0.001 g), and t is the time in days. Because mean daily food consumption and SGRw are a function of body size in fish, repeated measures ANCOVA was used to compare the trajectories of SGRw and food consumption over the weeks of refeeding. In the repeated measures design, feeding regime and infection status were the between-subject factors and weeks the within-subject factor. Weight at the end of the deprivation period was used as the body size covariate. To gain additional information on temporal aspects of re-alimentation and growth, one-factor ANOVAs were carried out to examine group differences on SGRw and food intake on selected dates. Significant differences between groups were identified using Fisher's pairwise comparisons

The number and total weight of plerocercoids recovered from fish at the end of the experiment were each analysed by two-factor ANCOVA, using final length as the covariate. All lengths and weights were log-transformed before the analyses to stabilize variances and to reflect the allometric relationships between variables.

Results

Weight

Body weight at the start of the experiment did not differ significantly between infected and uninfected fish ($F_{[1,18]}$ = 1.56, P = 0.23) or between fish that were to experience the deprived or continually fed treatment ($F_{[1,18]}$ = 0.01, P = 0.91). By the end of the deprivation period (week 4), feeding regime had a significant effect on body weight ($F_{[1,17]}$ = 73.05, P < 0.0005), with the deprived groups having a lower body weight than the continually fed groups (Fig. 1). There was no significant effect of infection status on weight at the end of the deprivation period ($F_{[1,17]}$ = 0.17, P = 0.68), nor was there a significant feeding regime × infection status in-

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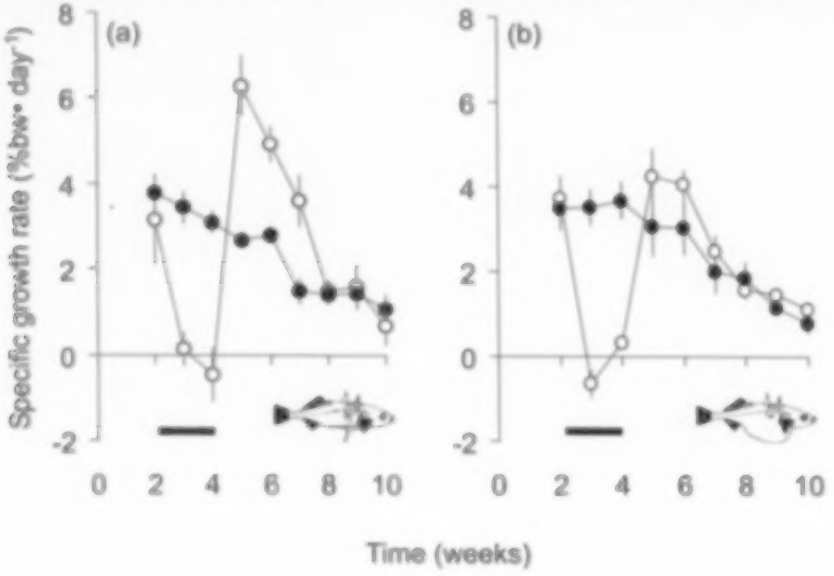
Fig. 2. The specific growth rates, measured as percent increase in body weight per day, of (*a*) noninfected and (*b*) experimentally infected threespine sticklebacks (*Gasterosteus aculeatus*) held under continual feeding conditions (●) or under a compensatory growth regime incorporating a 2-week period of food deprivation denoted by the horizontal bar (○). Data points are means ± standard error.



teraction ($F_{[1,17]} = 0.01$, $P = 0.91$). Thus, at the end of the food deprivation period, the deprived groups had experienced a period of growth depression.

Over the refeeding period, weight was significantly affected by a feeding regime × infection status × weeks interaction ($F_{[6,108]} = 3.344$, $P = 0.005$). This interaction arose because infected and uninfected fish differed in their capacity to mount a CG response. The weight of fish in the UD group had converged on that of fish in the UC group by week 7 and had shown complete compensation by the end of the refeeding period (Fig. 1*a*). The final weights of UD fish did not significantly differ from those of UC fish ($F_{[1,9]} = 0.07$, $P = 0.803$). The weight of the ID group failed to converge on the trajectory of the IC group (Fig. 1*b*). When including parasite weight, final weight of the ID group fish tended to be lower than that of fish from the IC group ($F_{[1,7]} = 5.12$, $P = 0.057$). When parasite weight was removed from fish weight, there was an even stronger tendency for final weight of the ID fish to be lower than that of the IC group ($F_{[1,7]} = 5.52$, $P = 0.051$; Fig. 1*b*).

Condition

At the end of the deprivation period, both feeding regime ($F_{[1,17]} = 15.08$, $P = 0.0012$) and infection status ($F_{[1,17]} = 7.042$, $P = 0.02$) had significant effects on weight-at-length. For a given length, deprived fish therefore weighed less than continually fed fish, and parasitized fish (including parasite weight) weighed more than nonparasitized fish. There was no feeding regime × infection status interaction. After 1 week of refeeding, the regression slopes relating weight to length were not homogeneous, so the ANCOVA was terminated. After two weeks of refeeding, weight-at-length was still significantly lower in the deprived groups ($F_{[1,17]} = 5.725$, $P = 0.03$). But, thereafter, there were no significant treatment effects on weight-at-length among the four treatment groups.

The effects of deprivation and infection status on liver weight at the termination of the study were examined by ANCOVA, using final length as the covariate. There was a significant infection × ration interaction on adjusted-body-size liver weight, ($F_{[1,17]} = 4.862$, $P = 0.04$), with infected fish having a lower liver weight than uninfected fish only in the food deprivation treatment.

SGRw

In the first week of the experiment, when all groups were being fed ad libitum and to excess, there was no significant effect of infection status on SGRw ($F_{[1,20]} = 0.02$, $P = 0.90$; Fig. 2). Over the refeeding period, SGRw was significantly affected by a feeding regime × infection status × week interaction ($F_{[5,90]} = 2.437$, $P = 0.04$). This reflected the elevated SGRw shown by the UD group over the first 3 weeks of refeeding (Fig. 2). One-way analyses of SGRw at week 5, followed by post hoc testing for pairwise differences, showed that UD fish had a significantly higher SGRw than all other groups at this stage ($F_{[3,21]} = 8.56$, $P = 0.001$). There were no other significant differences between groups in SGRw at week 5. At weeks 6 and 7, the SGRw of UD fish was significantly higher than that of both ID and UC groups (week 6: $F_{[3,21]} = 6.00$, $P = 0.005$; week 7: $F_{[3,21]} = 4.32$, $P = 0.018$). There were no significant differences in SGRw between the ID and IC groups. Taken over all refeeding weeks, SGRw of deprived groups was significantly higher than that of continually fed groups ($F_{[1,18]} = 15.53$, $P = 0.001$). In all groups, there was a highly significant decline in SGRw over the weeks of refeeding ($F_{[5,90]} = 50.47$, $P < 10^{-6}$; Fig. 2).

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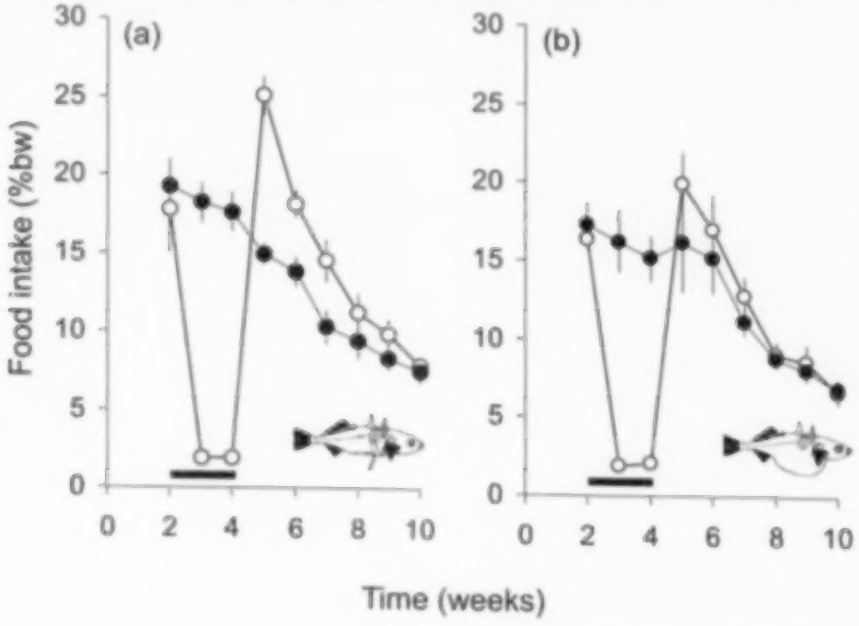
Fig. 3. The measured food intake of (*a*) noninfected and (*b*) experimentally infected threespine sticklebacks (*Gasterosteus aculeatus*) held under continual feeding conditions (●) or under a compensatory growth regime incorporating a 2-week period of food deprivation denoted by the horizontal bar (○). Data points are means ± standard error.



Food intake

Food intake was calculated as percent fish body weight; values were calculated daily to give mean consumption per week during each week of the experiment. Food consumption did not differ between groups in the first week of the experiment (P = 0.29). Food consumption during the refeeding phase was significantly affected by a feeding regime × infection status interaction ($F_{[1,17]}$ = 3.0115, P = 0.03). This reflected a hyperphagic response shown by UD fish in the refeeding phase that was not matched by the ID group (Fig. 3). A one-way ANOVA, with post hoc testing for pairwise differences, showed that the food intake of UD fish was significantly higher than that of all other groups in the first week of refeeding ($F_{[3,21]}$ = 6.31, P = 0.04). No other significant differences in food intake were found.

Parasite growth

Two fish from each treatment harboured single plerocercoids, while three from each treatment harboured multiple infections (range two–five plerocercoids). A two-way ANOVA, using a generalized linear model for unbalanced designs, was used to test for differences in infection characteristics between singly and multiply infected fish. Multiply infected fish (i.e., harbouring greater than 1 plerocercoid) exhibited significantly higher total parasite weight (TPW) than singly infected fish ($F_{[1,9]}$ = 23.95, P = 0.003). However, there was no effect of deprivation on TPW ($F_{[1,9]}$ = 0.38, P = 0.562), nor was there a significant infection level × feeding regime interaction on TPW ($F_{[1,9]}$ = 1.94, P = 0.214). Near identical results were generated when using parasite index (PI = TPW/(weight of infected fish including TPW); Arme and Owen 1967) as the response variable instead of TPW. PI of ID fish ranged from 0.08 to 0.22 (mean = 0.16), while the PI of IC fish ranged from 0.09 to 0.19 (mean = 0.15). Pooling data from singly and multiply infected fish, there was no significant effect of deprivation on body-size-adjusted TPW (P = 0.944).

Discussion

Parasites can have important impacts on fish growth in natural populations (e.g., Kennedy et al. 2001), and a number of studies have recently investigated the effects of experimental infection with microparasites and macroparasites on growth in fish (Saksvik et al. 2001; Blanar et al. 2005; Khan 2005). However, there have been few studies that have examined the impacts of experimental parasitic infections on patterns of growth in individual fish where intake has been precisely measured. Furthermore, no studies to date have examined the ability of infected fish to exhibit CG in response to variable food availability. Here, we have provided the first demonstration that the capacity of individual sticklebacks to undertake CG responses following a period of food-deprivation is significantly impaired by experimental *S. solidus* infection. We have shown that the effect of *S. solidus* is strongest during a narrow period after refeeding commences and that this short, but significant, reduction in capacity for CG does not allow full host recovery from food deprivation. In addition we have identified the likely mechanism involved. Experimentally infected fish have a reduced capacity to achieve high levels of hyperphagia on refeeding following the period of growth deprivation.

The capacity of healthy fish to display CG responses following food deprivation is well established (see Ali et al. 2003 for review). In the present study, 2 weeks of food deprivation were sufficient to generate significant body weight differences between deprived and continually fed groups.

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The time taken for deprived and uninfected sticklebacks to fully compensate (~3 weeks) and the hyperphagic responses shown were comparable with the patterns found previously (Ali and Wootton 1998; Zhu et al. 2001). In contrast, by the end of the study, deprived, parasitized sticklebacks had only attained 80% of the weight of continually fed, infected fish.

Why did infected fish not exhibit levels of hyperphagia comparable with noninfected fish on refeeding? One possibility is that the hyperphagic response of infected fish might have been limited because of morbidity associated with infection; sick hosts commonly suffer reduced appetite (e.g., rainbow trout (*Oncorhynchus mykiss*) infected with *Cryptobia salmositica*; Lowe-Jinde and Zimmerman 1991). However, this seems unlikely, since sticklebacks infected with *S. solidus* typically approach food and feed readily (e.g., Barber and Ruxton 1998). Alternatively, physiological processes relating to the ratio of reserve:structural materials (Broekhuizen et al. 1994) and lipid storage (Jobling and Johansen 1999; Johansen et al. 2002) might have influenced the strength of hyperphagia elicited. If some aspect of the body composition of infected fish more closely resembles that of a well-fed than of a starved fish, their hyperphagic response could be weakened. However, we consider this to be unlikely, since roach (*Rutilus rutilus*) infected with plerocercoids of the closely related pseudophyllidean *Ligula intestinalis* have an amino acid composition that is consistent with that of starved fish (Soutter et al. 1980). Another possibility is that infected fish may be unable to exhibit extreme hyperphagia because of physical constraints imposed by the parasite. Plerocercoids frequently attain 40% of the host's body weight (Hopkins and Smyth 1951; Arme and Owen 1967), and the presence of plerocercoids in the body cavity may restrict stomach expansion, because food intake is inversely related to the relative plerocercoid weight (Milinski 1985; Cunningham et al. 1994). Although plerocercoids in this study would not have been so large at the time of refeeding, a recent study has indicated that plerocercoids contributing at least 20% of the hosts weight can significantly reduce meal size in infected sticklebacks (Wright et al. 2006).

Finally, it is possible that the limited hyperphagia of infected fish may represent an adaptive strategy of either the host or the parasite or an interaction between the two. It is possible that host hyperphagia could have differential consequences for the growth and fitness of hosts and their parasites. One possibility, because *S. solidus* plerocercoids grow bigger in host sticklebacks that exhibit higher growth rates (Barber 2005), is that high levels of nutrient availability generated by extreme hyperphagia might benefit parasites more than hosts. In such a case, host responses to infection that restrict nutrient intake might be adaptive, since they may reduce parasite growth. Alternatively, if hosts are able to outgrow their parasites, as has previously been suggested (Aeschlimann et al. 2000), or use extra nutrients to fuel immune responses against them, then limiting the intake of hosts could be a fitness-maximizing strategy of parasites. Furthermore, because achieving the high growth rates necessary for compensation is apparently associated with a reduction in scale strength (Arendt et al. 2001), an increased risk of intraspecific aggression (Nicieza and Metcalfe 1999), long-term growth problems (Morgan and Metcalfe 2001), and ultimately lifespan (Metcalfe and Monaghan 2003), parasites that prevent CG responses may increase host longevity and therefore their own potential for growth. Further research examining the consequences of differential host nutrient intake for the growth and energetics of host–parasite systems is needed to better understand the likely fitness consequences of limited hyperphagia and impaired CG responses in parasitized fish.

Even with relatively small sample sizes, our study has shown that infection with *S. solidus* can inhibit the CG of host sticklebacks. The associated low statistical power — a consequence of the small sample sizes caused by the low rates of infection — may mean that other, more subtle effects of infection on growth and appetite were not detected. However, our data also show that while food deprivation clearly affected the growth of infected sticklebacks, parasite growth appeared to be conserved in deprived and infected fish, which developed plerocercoids as large as continually fed fish by the end of the study. Therefore, despite the fact that infections appeared to impair the capacity of host fish to undertake CG, there was no evidence that host food deprivation had an impact on parasite growth. Parasites were, therefore, either not sensitive to poor early host nutrition or were capable of undertaking their own compensatory responses using host-derived nutrients. Also, while deprivation had no effect on terminal liver weight of uninfected fish (see also Zhu et al. 2001), infected and deprived fish did exhibit reduced liver weights, suggesting that infection interacts significantly with temporal food availability to generate observed patterns of energetic condition. These results provide further evidence that the implications of parasitic infections for the health and fitness of host organisms are highly dependent on local environmental conditions (e.g., Candolin and Voigt 2001).

In conclusion, we have demonstrated for the first time that CG responses can be impaired by parasitic infection, that experimental infections can have more severe consequences for hosts under natural, fluctuating food availability, and that the failure of the CG response in experimentally infected sticklebacks is likely to be due to an infection-induced weakening of the hyperphagic response. Consequently, we suggest that the growth effects of parasitism demonstrated under fluctuating food availability represent a hitherto hidden cost of infection that may be highly relevant in natural environments. Future studies should focus on experimental examinations of interactions between infection status and variable environmental conditions to better understand the likely effects of parasites in natural environments.

Acknowledgements

HAW is grateful for Ph.D. studentship funding from the Institute of Biological Sciences, University of Wales Aberystwyth. IB was in receipt of Natural Environment Research Council (NERC) fellowships (GT/5/98/6/FS and NER/I/S/2000/00971) during the research. We thank the Editor and two referees for perceptive and helpful comments on the manuscript. Experimental parasitic infections and food ration manipulation was carried out in accordance with local and national welfare guidelines, under UK Home Office licence PPL40/2240.

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Consequences of variations in carrying capacity or migration for the perception of Atlantic bluefin tuna (*Thunnus thynnus*) population dynamics[1]

Jean-Marc Fromentin and Laurence T. Kell

Abstract: Spectacular long-term cycles (around 110 years), independent of human exploitation, have been seen in historical catches of Atlantic bluefin tuna (*Thunnus thynnus*). Previous studies indicated that such variations could have been generated by contrasting but equally plausible dynamic processes, i.e., changes in carrying capacity or migration. A simulation framework was therefore used to test whether the International Commission for the Conservation of Atlantic Tuna stock assessment model, i.e., a virtual population analysis (VPA), can capture such dynamics. The main outcome is that knowledge of the underlying process is crucial, because distinct hypotheses lead to different population dynamics and contrasting performances of the stock assessment model. The VPA is indeed able to reconstruct accurately the historical stock parameters under the carrying-capacity hypothesis, but not under the migratory hypothesis, for which there is often strong bias (up to 500%) in absolute values and in trends of spawning stock biomass and F. Furthermore, it was shown that (*i*) different phases between exploitation and long-term cycle can induce contrasting terminal F for a same effort and (*ii*) that there was considerable confounding between the dynamics and increasing effort (as currently seen). We conclude that it is difficult to infer the actual dynamics on the basis of commercial catch data and that novel fishery-independent observation is needed.

Résumé : Les captures historiques du thon rouge atlantique (*Thunnus thynnus*) présentent de spectaculaires fluctuations à long terme (de l'ordre de 110 ans) qui semblent indépendantes de l'exploitation. Des travaux antérieurs indiquent que les causes de ces variations pourraient résulter de processus dynamiques différents, mais également probables, comme des changements dans la capacité de charge ou de migration. Un modèle de simulation a été utilisé pour tester si le modèle d'évaluation de stock de la CICTA (Commission Internationale pour la Conservation des Thonidés de l'Atlantique), i.e., une analyse des populations virtuelles (APV), peut rendre compte de telles dynamiques. Le principal résultat est que la connaissance des processus sous-jacents est cruciale, parce que des hypothèses distinctes conduisent à des dynamiques de populations différentes et à des performances du modèle d'évaluation contrastées. L'APV est en effet capable d'estimer correctement les principaux paramètres d'intérêt sous l'hypothèse de la capacité de charge, mais pas sous l'hypothèse migratoire, pour laquelle apparaissent fréquemment de forts biais (jusqu'à 500 %) dans les valeurs absolues et les tendances de la biomasse reproductrice et de F. De plus, on constate que (*i*) des différences de phase entre exploitation et cycle à long terme peuvent générer des F terminaux très différents pour un même effort et (*ii*) qu'il y avait de fortes interactions entre la dynamique de population et l'effort (surtout si ce dernier est croissant comme cela est actuellement le cas). Nous concluons, qu'il est difficile de déduire la dynamique actuelle à partir des données commerciales de pêche et que des suivis originaux et indépendants de la pêche sont nécessaires.

Introduction

Fish stocks can fluctuate extensively over a large range of spatial and temporal scales independently of human exploitation (Hjort 1914; Cushing 1995). Such fluctuations are often ascribed to stochastic variations in key processes, such as recruitment, growth, predation, or migration, in relation to environmental modifications (e.g., Lehodey et al. 1997; Bailey 2000; Köster et al. 2005). A recent study on historical catches from the ancestral Atlantic and Mediterranean trap fisheries showed that there had been spectacular long-term fluctuations in bluefin tuna (*Thunnus thynnus*) catches over the last four centuries (Ravier and Fromentin 2001). These pseudo-cyclic variations of 100–120 years, accounting for more than 50% of the variance of the time series, were synchronous all around the western Mediterranean and near North Atlantic (i.e., between sites more than 2000 km apart), so that they were likely to reflect fluctuations in bluefin tuna

Received 4 April 2006. Accepted 17 December 2006. Published on the NRC Research Press Web site at cjfas.nrc.ca on 21 June 2007. J19256

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population migrating annually in the Mediterranean for spawning (Ravier and Fromentin 2001). Further studies postulated that such long-term fluctuations could alternatively arise from resonant effects, attributable to a combination of stochastic recruitment and long life span (Bjørnstad et al. 2004), or from modifications in migration patterns caused by changes in sea temperature (Ravier and Fromentin 2004).

Whatever the underlying processes, significant fluctuations in carrying capacity or migration patterns can violate various model assumptions used to assess the stock and so affect our perception of stock status (Fromentin et al. 2000; Kell et al. 2000). For instance, the stock assessment of bluefin tuna, which is currently performed by the scientific committee of the International Commission for the Conservation of Atlantic Tunas (ICCAT), considers a single stock for the East Atlantic and Mediterranean Sea. The stock assessment model, based on virtual population analysis (i.e., an ADAPT-VPA approach; Porch 1997), does not reflect the fact that spawning only occurs in specific locations of the Mediterranean Sea. Consequently, potential year-to-year variations in spawning migrations between the East Atlantic and the Mediterranean cannot be quantified, although they may affect catch rates. Furthermore, time series used in stock assessment only extend for 30 years, which is a small fraction of the full natural cycle (100–120 years). Therefore a simulation framework (Kell et al. 2003) was used to evaluate the effect of the potential bias associated with changes in either carrying capacity or migration on the ICCAT stock assessment.

To do so, we modelled a bluefin tuna population displaying either variations in carrying capacity or changes in migration; for each population model, catch and catch per unit effort (CPUE) were sampled and the standard ICCAT stock assessment model was run. This allowed the performances of the stock assessment model to be evaluated for uncertainty about the true dynamic processes.

Although the current study is based on Atlantic bluefin tuna because data on historical catches are available for this population, the study has broad implications for stock assessment and management of other species.

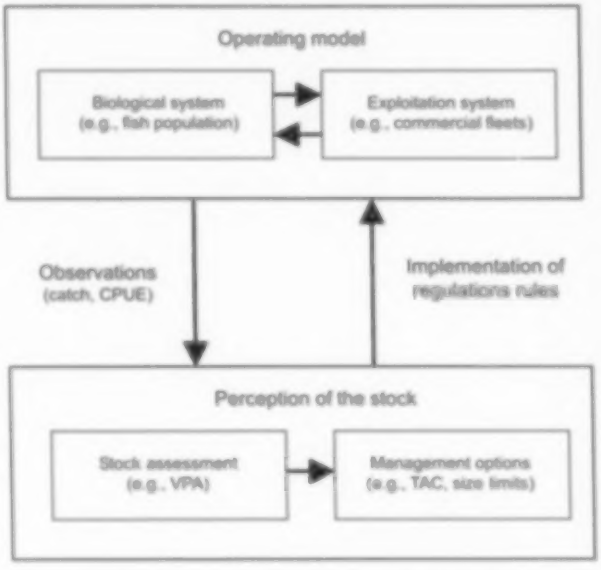
Material and methods

Simulation model framework

The simulation framework (Kell et al. 2000, 2003) was used to build (*i*) an operating model (OM) that represents alternative plausible hypotheses about stock and fishery dynamics, allowing integration of a higher level of complexity and knowledge than used within stock assessment models; (*ii*) an observation model that describes how pseudo-data are sampled from the operating model; and (*iii*) a stock assessment and management model to derive estimates of stock status from the pseudo-data (Fig. 1).

Within this framework, three different types of variable are considered. In the operating model, the variables are controlled, i.e., fixed by the operator, so decisions have to be taken on biological parameters. In the observation model, the variables are observed, i.e., deduced from the sampling model. In the stock assessment and management model, the variables are estimated (and represent the dependent variables).

Fig. 1. Conceptual framework of the simulation model that considers (*i*) an operating model that represents alternative plausible hypotheses about stock and fishery dynamics, (*ii*) an observation model that describes how pseudo-data are sampled from the operating model, and (*iii*) stock assessment and management model to derive estimates of stock status from the pseudo-data.



The approach is therefore able to model the full variety of uncertainty characterised by Rosenberg and Restrepo (1994): in the operating model, process error attributable to natural variations in dynamic processes (recruitment, growth, natural mortality, etc.); in the observation model, measurement error generated when collecting observations from a population; in the stock assessment and management estimation, error that arises from trying to model the dynamic process. The approach is also able to model important interactions and feedback processes between the operating model and stock assessment and management model, i.e., the consequences of model mis-specification, because the assumption used within stock assessment may not be the same as in the operating model, and implementation error, because management actions are never implemented perfectly. However, feedback was not included in this case because the objective was to investigate how well current stock assessment assumptions and models used for bluefin tuna capture the dynamics of the stock, not to develop an appropriate management strategy.

Basis of the operating models

The objective of this study is to use a simulation framework to evaluate whether a stock assessment model based on virtual population analysis (VPA) can capture the dynamics of stocks where ecological processes may generate long-term fluctuations in catches and, in particular, to determine how such variations may affect our perception of stock status and our ability to manage it based on relatively

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short-term time series of data. Therefore an operating model was constructed on the basis of the following age-structured equation:

$$N_{a,t} = N_{a-1,t-1}\, e^{-Z_{a,t}}$$

where $N_{a,t}$ is the number of fish of age a at time t, $Z_{a,t}$ is the total mortality from age $a-1$ to age a ($Z_{a,t} = M_a + F_{a,t}$, where M_a is the natural mortality at age a and $F_{a,t}$ is the fishing mortality at age a in year t). Life history traits of the East Atlantic and Mediterranean population are those described in Fromentin and Fonteneau (2001) and ICCAT (2003): (*i*) annual spawning (1 cohort per year), (*ii*) 50% maturity at age 4, 100% maturity at ages 5+ (i.e., immature before age 4), (*iii*) fecundity is linearly proportional to weight, (*iv*) growth following the von Berttalanffy equation used in the ICCAT working group (with the following parameters: $L_\infty = 318.85$, $k = 0.093$, $t_0 = -0.97$), (*v*) length–weight relationship used in the ICCAT working group ($W = 2.95 \cdot 10^{-5} \cdot L^{2.899}$), (*vi*) life span of 20 years, and (*vii*) age-specific, but time-invariant, natural mortality based on tagging experiments on the southern bluefin tuna and used in the ICCAT working group (i.e., $M = 0.49$ for age 1, 0.24 for ages 2–5, 0.2 for age 6, 0.175 for age 7, 0.15 for age 8, 0.125 for age 9, and 0.1 for ages 10–20).

The population dynamics of the OM was further based on a Beverton–Holt stock–recruitment relationship (Beverton and Holt 1957) reparameterised for a given M, growth, and maturity at age in terms of steepness (τ) and virgin biomass (γ) (Francis 1992). Steepness is the fraction of the virgin recruitment (R_γ) expected when spawning stock biomass (SSB) has been reduced to 20% of its maximum (i.e., $R = \tau R_\gamma$ when SSB = $\gamma/5$) and represents the resilience of the stock to exploitation. In the absence of information on steepness, τ was set at 0.75 and 0.9, i.e., a range of values that make biological sense for bluefin tuna.

The expected virgin biomass was arbitrarily set at 10^6 tonnes (t), because the study was intended to provide strategic rather than tactical advice (i.e., the consequences of making different decisions rather than setting specific quotas), and results are presented as relative rather than absolute.

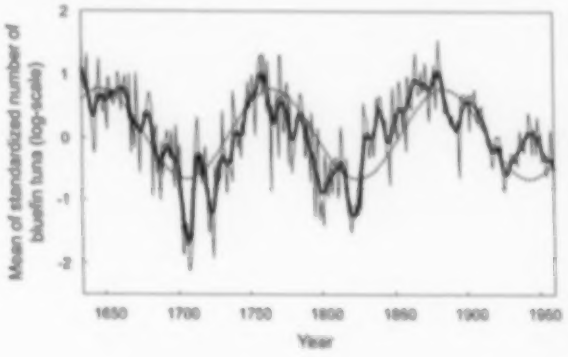
The purpose of the operating model is not to reproduce the entire complexity of bluefin tuna biology and ecology, which would be highly subjective because our knowledge of bluefin tuna ecology relies mainly on a variety of unproven hypotheses (Fromentin and Powers 2005), but to define plausible hypothesis about population dynamics and then to implement the processes of interest, i.e., changes in carrying capacity and migration pattern, to finally measure the effect of the potential bias associated with the underlying assumption of the current ICCAT stock assessment process.

Operating model for carrying capacity (H_k)

This model assumes that the long-term fluctuations observed in trap catches reflect changes in the carrying capacity or virgin biomass (λ_t) that are due to a combination of stochastic recruitment and long life span (Bjørnstad et al. 2004). λ_t is assumed to vary with respect to time as

$$\lambda_t = \varpi \sin(\theta + \delta t)$$

Fig. 2. Historical catch time series from Atlantic and Mediterranean trap fisheries (thin line) with the smoothing time series (bold line; after Ravier and Fromentin 2001) and fitted sign wave (dotted line).



where ϖ, θ, and δ were chosen to reflect the observed long-term trend in catches (Fig. 2). Note that λ_t is scaled so as to always be positive.

Operating model for migration (H_M)

According to Ravier and Fromentin (2004), long-term variations in trap catches may alternatively result from changes in migratory patterns that would affect the proportion of mature bluefin tuna entering the Mediterranean Sea each year to reproduce. Knowing that (*i*) most fishing effort is in the Mediterranean (80% of the total catch occurs in the Mediterranean Sea) and (*ii*) the vulnerability of bluefin tuna to fishing is much higher in the Mediterranean Sea than in the Atlantic (because it occurs many on spawning aggregations), year-to-year variations in spawning migration between the East Atlantic and the Mediterranean Sea induce concomitant variations in the fraction of the population available to fishing gears (see ICCAT 2007). It may be thus approximated as the proportion of the population being vulnerable to fishing, i.e.,

$$N_{a+1,t+1} = A_t \cdot N_{a,t} \cdot e^{(-M_a - F_{a,t})} + (1 - A_t) \cdot N_{a,t} \cdot e^{(-M_a)}$$

where A_t is the proportion of the population available or vulnerable to fishing ($1 - A_t$ is thus equated to the unexploited or cryptic biomass, which is a reasonable simplification acknowledging the relatively low level of effort in the Atlantic in comparison to the Mediterranean). It was assumed that A_t was a sinusoidal function of time (constrained to be positive and to vary between 20% and 80%):

$$A_t = \varpi \sin(\theta + \delta t)$$

where ϖ, θ, and δ were again chosen to reflect the long-term trend in catches (Fig. 2).

Estimating population trends

As the dominant signal, i.e., low frequencies, was the process of interest, the smoothed time series of trap catches (Fig. 2) was used to estimate the time-varying population parameters. In both models, the yield was predicted using an age-structured forward projection, with a selectivity pattern similar to the present exploitation (ICCAT 2003). The sum

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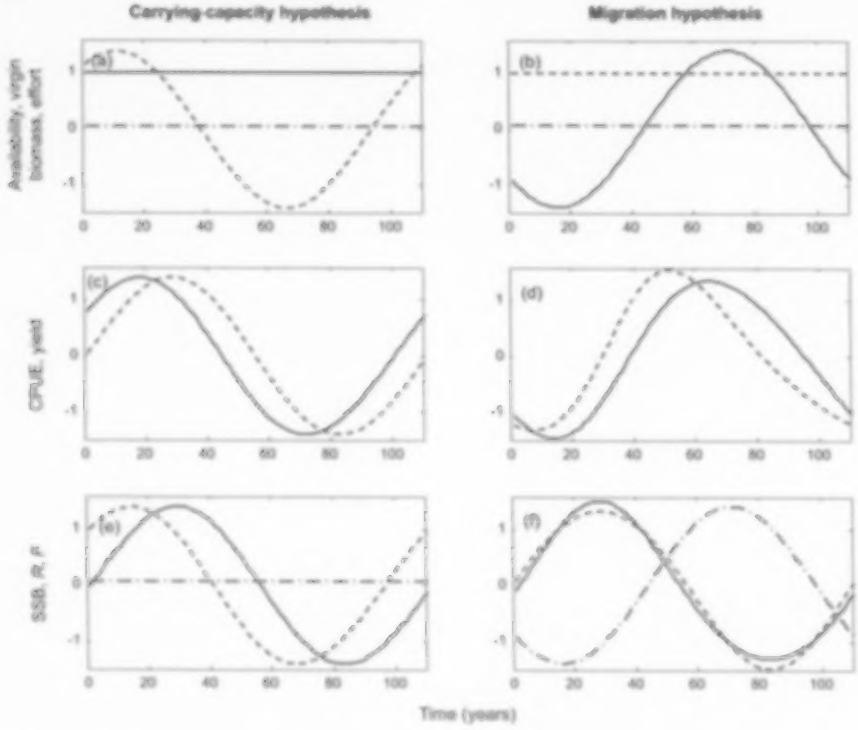
Fig. 3. Outputs from the operating model (OM) for a full cycle (110 years) with constant fishing mortality (F) equivalent to F at maximum sustainable yield (F_{MSY}) and a steepness of 0.75. (*a*) Standardized time series of availability (solid line), virgin biomass (broken line), and effort (dotted–dashed line) for the carrying-capacity hypothesis (H_K); (*b*) same as (*a*) for the migration hypothesis (H_M); (*c*) standardized time series of capture per unit effort (CPUE, solid line) and yield (broken line) for H_K; (*d*) same as (*c*) for H_M; (*e*) standardized time series of spawning stock biomass (solid line), recruitment (broken line), and F (dotted–dashed line) for H_K; (*f*) same as (*e*) for H_M.



of squares of the difference in the observed trend was scaled so that the difference between the smoothed yield and predicted yields were minimized.

The amplitude of the trend was a given fraction of MSY and fixed so that it was similar under both hypotheses (H_K and H_M) and in agreement with the variability observed in catches over the 1910–1930 (Ravier and Fromentin 2002) and 1950–1990 periods (i.e., a rough CV of ~40%).

Sensitivity runs

Finally, decisions have also to be taken with respect to the historical fishing mortality (relative to MSY) and the starting point of exploitation relative to the natural cycle. For the first point, we considered four different historical Fs: constant effort corresponding to F = 50% of F_{MSY}, constant effort corresponding to $F = F_{MSY}$, constant effort corresponding to F = 150% of F_{MSY}, and linear increase in effort corresponding to an increase in F from 50% of F_{MSY} to 250% of F_{MSY} over a full population cycle (i.e., 110 years).

For the second point, we examined four different starting points (or phases of the cycle), i.e., yield in year 1 was at maximum of the natural cycle, middle of the decreasing trend, minimum of the natural cycle, and middle of the increasing trend.

Monte Carlo simulations, where process and observation errors are modelled as random variables, were also considered as part of the experimental design. However, stochastic results are presented only in Kell and Fromentin (2007) to evaluate the robustness of the management strategies.

Results

All the sensitivity runs (including the historical fishing mortality and starting points, as well as the two steepness values) generate 32 simulations for each hypothesis (H_K and H_M). Presenting all these 64 simulations will be lengthy and will further create redundancy. Therefore, the results are mainly based on some specific cases to stress the most important outputs, but the results of all the sensitivity runs are finally summarised and compared in the last figure of this section.

Operating models with constant effort

To illustrate the contrast in dynamics under the two hypotheses for a full cycle of 110 years, the results from a single scenario, with constant effort (equal to F_{MSY}) and a steepness of 0.75, are presented (Fig. 3). Interpretation of the results under H_K (where virgin biomass is the fluctuating control variable) are relatively straightforward (Figs. 3*a*, 3*c*, 3*e*). As expected, CPUE, yield, and recruitment (R) vary in synchrony with virgin biomass (note that the catch is confounded with CPUE because effort is constant). An in-

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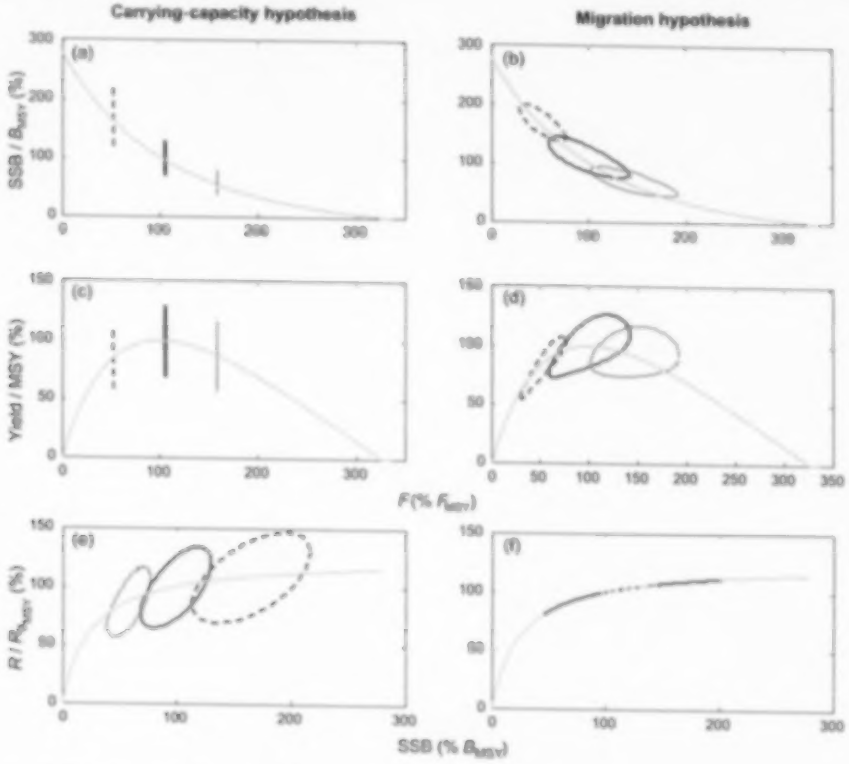
Fig. 4. Outputs from the operating model (OM) for a full cycle (110 years) with steepness of 0.75 and different levels of fishing mortality (F): equivalent to F at maximum sustainable yield (F_{MSY}, solid line), 50% of F_{MSY} (broken line), and 150% of F_{MSY} (dotted line). (*a*) F (relative to F_{MSY}) against spawning stock biomass (SSB) relative to spawning stock biomass at MSY (B_{MSY}) for carrying-capacity hypothesis (H_K); (*b*) fishing mortality against SSB for migration hypothesis (H_M); (*c*) F (relative to F_{MSY}) against yield (relative to MSY) for H_K; (*d*) F against yield for H_M; (*e*) SSB (relative to B_{MSY}) against recruitment (R relative to R_{BMSY}) for H_K; (*f*) SSB against R for H_M. Shaded curves display for each plot the values that would be expected under equilibrium for the virgin biomass corresponding to the mean value used in the scenarios.



crease or decline in R induces a subsequent increase or decline in SSB and yield with a lag of about 15 years (Figs. 3*c*, 3*e*). The fact that the yield and CPUE (or catch) are slightly delayed simply reflects changes in the composition of the catches caused by variations in R, because older fish weigh more (Fig. 3*c*). Under H_M, when availability is the fluctuating control variable (Fig. 3*b*), the results are more complex. Although effort is constant, F fluctuates owing to the varying proportion of the population available to fishing: it increases as the proportion of the population available to fishing increases (Fig. 3*f*). Variations in fishing mortality and availability are, therefore, synchronous (Figs. 3*b*, 3*f*). Also in contrast to the situation with H_K, synchrony is seen between SSB and R (Fig. 3*f*). Furthermore, the phases of SSB and R are now in opposition to those of the control variable (and F). SSB and R are high when the availability to fishing is low, and vice versa. This results from the stock not being in equilibrium, and although fishing mortality is a function of current availability, year-class strength is a function of historic availability. Variations in CPUE (or catch) and yield result from both the fraction being harvested (i.e., availability) and the population size (or SSB), so CPUE and yields peak after the maximum SSB, but before F does. However, the yield is more dependent on SSB than on CPUE (or catch), which generates a slight delay between both variables (Fig. 3*d*).

Differences between H_K and H_M are even more obvious when plotting SSB or yield against fishing mortality and recruitment against SSB (for which we still consider a steepness of 0.75, but the three scenarios with constant effort, i.e., at 50% of F_{MSY}, F_{MSY}, and 150% of F_{MSY}; Fig. 4). Under H_K, the scatter plots of SSB and yield against fishing mortality display a vertical line, because fishing mortality is a linear function of effort (which is constant) and yield or SSB vary (reflecting long-term variations in virgin biomass and hence in productivity; Figs. 4*a*, 4*c*). Note that the lag of about 15 years between R and SSB generates a loop of solutions in contrast to what is expected under equilibrium. For a given SSB, there are two values of recruitment (and vice versa). For each of the three efforts, there is a distinct range of possible SSB–R pairs (which move along the expected stock–recruitment curves; Fig. 4*e*). In contrast, for H_M, fishing mortality varies even when effort is constant, and there is a delay between F and SSB (or yield). Consequently, there are two dissimilar and contrasting values of yield and SSB for a given F (Figs. 4*b*, 4*d*). There is therefore a range of possible F–SSB and F–yield pairs for a given effort (which also move along the curves of expected values). As SSB and

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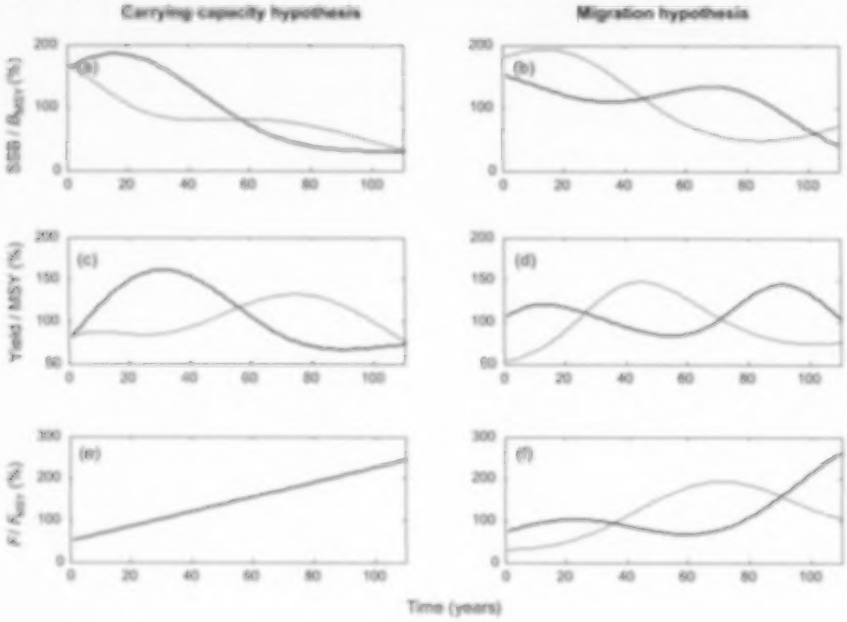
Fig. 5. Outputs from the operating model (OM) for a full cycle (110 years) with steepness of 0.75, increasing fishing mortality (F, from 50% F at maximum sustainable yield, F_{MSY}, to 250% F_{MSY}) and two different starting points, i.e., starting at high (solid line) or low (dotted line) carrying capacity or availability. (*a*) Time series of spawning stock biomass (SSB) relative to spawning stock biomass at MSY (B_{MSY}) under carrying-capacity hypothesis (H_K); (*b*) SSB under the migration hypothesis (H_M); (*c*) time series of yield (relative to MSY) under H_K; (*d*) yield under H_M; (*e*) time series of F (relative to F_{MSY}) under H_K; (*f*) F under H_M.



R remain roughly synchronous under H_M, the relationship between both variables corresponds to that expected under equilibrium (Fig. 4*f*). A higher steepness of 0.9 does not further change the behaviour and differences between H_K and H_M, but simply moves all the curves along the x and y axes. In conclusion, the underlying mechanisms to the long-term fluctuations in catches really matter, as H_K and H_M lead to contrasting results, especially regarding F (constant in one case and fluctuating in the other) and the differences of phase between SSB, R, yield, and F.

Operating models with increasing effort

The response of the two operating models to a linear increase in effort (leading to an increase in F from 50% of F_{MSY} to 250% of F_{MSY}) are explored in Fig. 5 for a steepness of 0.75 and two contrasting starting points, i.e., initially close to a maximum (solid line) and a minimum (broken line) in carrying capacity or availability. Increasing effort alters the long-term fluctuations in carrying capacity or availability that are observed under constant effort (especially in the second part of the cycle, which is generally masked; Figs. 5*a*, 5*b*, 5*c*, 5*d*). Differences are still seen between H_K and H_M and also within each hypothesis, depending on the starting conditions. Under H_K, there is a lag of about 15 years between yield and SSB when effort increases, whereas these are in phase under constant effort (Figs. 3*c*, 3*e*), which is due to year-class effects (Fig. 5*a*). Differences in starting conditions further generate distinct yield patterns under H_K (Fig. 5*c*): in one case, yields are relatively stable through time, whereas in the second case, they clearly display a dome-shaped curve (with more variability). Under H_M, differences in starting conditions are more acute and induce strong differences in the range of F. When the simulation starts (and ends) at low availability, fishing mortality is about F_{MSY} at the end of the series, whereas it exceeds 250% of F_{MSY} when starting at high availability (Fig. 5*d*). Again this is because availability and SSB are in opposite phase. As F is proportional to availability (see Fig. 3), F remains relatively low for initial and final low availability, because high values of effort are partially compensated for by low values of availability. For initial high availability, greatest effort coincides with greatest availability and generates very high F (Figs. 5*b*, 5*f*). This makes the final decreasing slope in yield more abrupt (Fig. 5*d*). If final SSBs are different (75% and 40% of B_{MSY} when starting at low and high availability, respectively), there are even stronger differences in the terminal trends in SSB (slightly positive in the former case, strongly negative in the latter; Fig. 5*b*). Finally, there is considerable confounding between the dynamics and increasing effort that makes it difficult to make any inference about the actual dynamics based on commercial catch data. The phases between exploitation and

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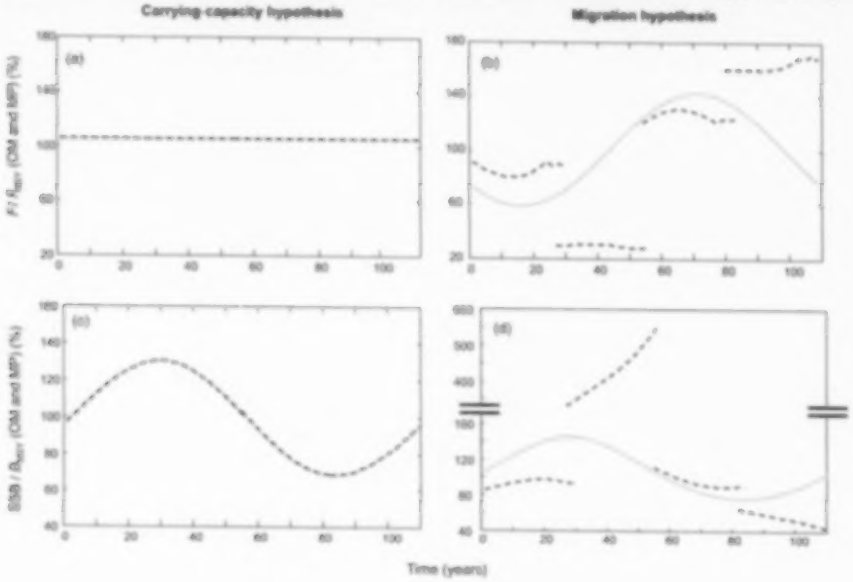
Fig. 6. Fishing mortality (F) and spawning stock biomass (SSB) from the operating model (shaded line) and estimated by the virtual population analysis (VPA, broken line) for both carrying-capacity hypothesis ((*a*) and (*c*)) and migration hypothesis ((*b*) and (*d*)), considering four different starting points (scenarios with constant historical $F = F$ at maximum sustainable yield, F_{MSY}, and steepness = 0.75).



natural cycle further induce contrasting outputs, especially for H_M, as the terminal F can vary by 250% for the same effort.

Consequences for stock assessment

To evaluate the consequences of these two operating models on our perception of stock status, catch-at-age and CPUE were sampled from the operating model (without observation error) for the most recent 30 years. We then used the same ADAPT-VPA used by the ICCAT working group (Porch 1997) to reconstruct the historical stock parameters of interest (i.e., SSB and F). The performance of VPA to both operating models is firstly evaluated for the scenarios with a constant effort (equivalent to F_{MSY}), a steepness of 0.75, and for four different starting points. In the case of H_K, VPA is always able to reconstruct the time series of SSB and fishing mortality accurately (both with respect to trends and absolute values; Figs. 6*a*, 6*c*). However, the reconstruction of the historical time series under H_M is more problematic (Figs. 6*b*, 6*d*), in particular because SSB, yield (and CPUE), and fishing mortality are not synchronous within the OM (see above). Consequently, there is in most cases a mismatch between the time series of auxiliary information (CPUE), catch, SSB, and fishing mortality over the stock assessment period, which induces strong biases in both trend and absolute values (that can even reach up to 500%; Fig. 6*d*). The trends in CPUE can, fortuitously, match those of SSB and F over a short period (such as the 30 years of the stock assessment period). In those cases (one in four of the scenarios), the estimates are more satisfactory (Figs. 6*b*, 6*d*). The other scenarios (with different fishing mortality patterns and higher steepness) are in agreement with the above findings. Finally, the ADAPT-VPA is generally able to reconstruct accurately the historical stock parameters under H_K, but not under H_M.

Let us finally consider the 64 scenarios (two hypotheses, two steepnesses, four historical Fs, and four starting points) to evaluate the main sources of the bias. To do so, we computed the ratio of the VPA to the OM quantities (SSB and F) of all scenarios (a value close to 1 indicating no bias) through box plots (Fig. 7). The results by hypothesis are clearly dissimilar (Fig. 7*a*), being unbiased (i.e., equal to 1) for all the cases (no variability) under H_K, but strongly biased under H_M, with high variability between cases (>300% in some cases for SSB). The results by steepness, constant historical Fs relative to F_{MSY}, and effort (constant versus increasing) did not display any special patterns (Figs. 7*b*, 7*c*, 7*d*). The results are generally unbiased, except for some cases when $F = 50\%$ or 150% of F_{MSY}. In other words, differences in steepness, historical Fs, and effort (i.e., constant or increasing) do not affect the performances of the VPA, whereas the differences in hypothesis strongly do. The box plots split by phases (or starting points; Fig. 7*e*) exhibit some strong differences, as the estimates of the VPA (especially those of SSB) are more biased for some phases ($\pi/2$ and $3\pi/2$) than others (e.g., 0). Note that for all the scenarios, the estimates of SSB are more biased than those of F. In conclusion, the performances of VPA depend firstly on the underlying process that generates long-term fluctuations in catch (i.e., H_K or H_M) and secondly on the starting point (i.e., when the exploitation starts along the natural long-term cycle).

Discussion

The main outcome of this study is that knowledge of the underlying process that generates long-term variations in

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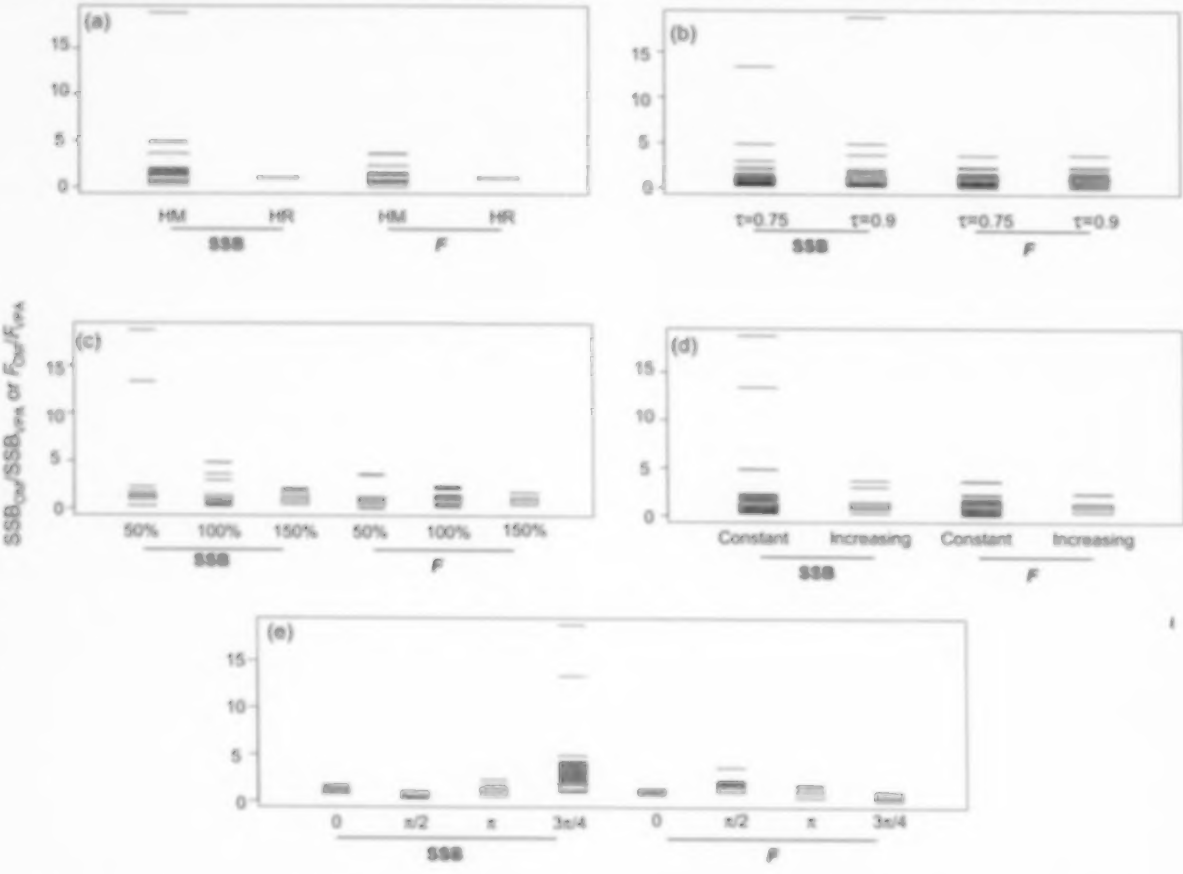
Fig. 7. Box plots of the ratios of spawning stock biomass (SSB) and fishing mortality (F) in operating models (OM) and virtual population analysis (VPA) for all the scenarios (ratios close to 1 indicate no bias or a good performance of the VPA). (*a*) Scenarios split by hypothesis (carrying-capacity hypothesis, H_K, versus migration hypothesis, H_M); (*b*) split by steepness ($\tau = 0.75$ and 0.9); (*c*) split by historical fishing mortality intensity (i.e., 50% of F at maximum sustainable yield (F_{MSY}), 100% F_{MSY}, 150% F_{MSY}); (*d*) split by constant versus increasing effort; and (*e*) split by starting points (i.e., phases between exploitation and natural long-term cycle).



catch is crucial for the current ICCAT assessment procedure because distinct processes (i.e., changes in carrying capacity or in migration) lead to different population dynamics and to contrasting performances of the stock assessment model.

When fluctuations in yield are attributable to changes in carrying capacity (H_K), fishing mortality is proportional to effort and SSB and yield fluctuates in synchrony because variation is driven by recruitment (with a lag of about 15 years). In contrast, under H_M, fishing mortality fluctuates even when effort is constant, because fishing mortality is proportional to and synchronous with availability. However, SSB and R (which are synchronous in this case) are in opposite phases with F under H_M. The cycles of yield and CPUE are intermediate between the availability – fishing mortality and SSB–recruitment cycles, because they are driven by both population size and F. Consequently, for a given effort, fishing mortality and hence SSB and yield vary. This gap between fishing mortality and stock size is a key feature in understanding differences in the perception of stock status (see below) and the key difference between H_M and H_K.

When fishing effort is increasing, the phases in the dynamic cycle also have a strong effect on the outputs of the operating models. This is because phase determines where in the cycle of SSB the system is, and depending on the phase, changes in SSB and yield can be of quite different magnitudes for the same effort. Under H_M, the phase strongly influences both the trend and the absolute values of F (and of SSB and yield). When high effort coincides with low availability, F remains relatively low because the high values of effort are partially compensated for by low values of availability, and vice versa. Increasing effort will thus always lead to a depleted stock under H_K (as F is directly proportional to effort), but not necessarily under H_M, because nonavailability of a component of the stock can act as a buffer against overexploitation. This observation is of particular interest with regard to the current exploitation of the Atlantic bluefin tuna, which has strongly increased over the last two decades (Fromentin and Powers 2005). Last ICCAT stock assessments (being partially based on VPA outputs) concluded to a severe overexploitation and overfishing of blue-

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fin tuna that could lead to a rapid fisheries and stock collapse (ICCAT 2003, 2007). If there is very little doubt that current fishing pressure is much too high and unsustainable (Fromentin and Powers 2005; ICCAT 2007), one may thus wonder how this population could have sustained such a long history (i.e., the last 25 years) of heavy exploitation. As we showed, our results suggest that under the migration hypothesis, a high level of exploitation can finally generate moderate F if high values of effort coincide with low availability (but determining the phase of the cycle remains difficult without fishery-independent information). However, this supposition would imply that availability is currently increasing, and therefore F is going to increase sharply and strongly in the coming years (even if effort stays constant). So whatever the underlying mechanism, it appears crucial to significantly reduce fishing effort on bluefin tuna.

The performance of VPA also depends on the underlying process that generates long-term fluctuations in catch. VPA can indeed accurately reconstruct the time series of SSB and fishing mortality (both trends and absolute values) under H_K, because the catch-at-age matrix and CPUE time series correctly reflect changes in carrying capacity. In contrast, VPA fails in most cases under H_M, where there is strong bias (up to 500%) in the absolute values and also in trends of SSB and F. Under H_M, the perception of the stock is generally erroneous, because availability to fishing remains unknown (neither the catch-at-age matrix nor the CPUE time-series can reflect such changes) and because the process induces a strong delay between fishing mortality and SSB (or recruitment). Indeed, population dynamics models assume that stock size varies in synchrony with fishing mortality because all individuals of a given stock are supposed to be equally vulnerable to fishing (Hilborn and Walters 1992). When postulating potential changes in availability (which has been also assumed for other tuna species; see Fonteneau et al. 1998), this hypothesis is violated, which makes classical population models unreliable.

The recent ICCAT reports stressed the potential biases in VPA outputs because of strong uncertainties in catch-at-age and CPUE indices (ICCAT 2003, 2007). Our results indicated that the VPA performances could be further seriously impaired if the long-term variations in catches are due to changes in migration or availability. It is therefore crucial to understand which underlying process induces long-term variations in catches to be able to recreate population dynamics, which primarily depends on our ability to collect novel fishery-independent observations as, in the case of bluefin tuna, data and knowledge are currently much more limiting than models. However, collecting fisheries-independent information on recruitment and SSB, which is regularly carried out for various pelagic or demersal fish stocks (e.g., Pennington and Strømme 1998; Gudmundsson 2004), is difficult for Atlantic bluefin tuna because of the species' highly migratory nature, wide spatial distribution, and complex, but still largely unknown, behaviour (Mather et al. 1995; Royer et al. 2004; Schick et al. 2004). New technologies have nonetheless opened avenues of great interest to tackle such a challenge. The most popular is undoubtedly electronic tagging (e.g., Block et al. 2005), which in the near future (if effort is enforced in the Mediterranean Sea) could allow estimation of migratory behaviour. The combination of a fixed hydrophone array across the Gibraltar Strait with acoustic tags is another (audacious) option. Such a system, which would be closer to those recently set up to track Atlantic salmon (e.g., Lacroix and McCurdy 1996), could allow the quantification of the migratory flux of bluefin tuna through Gibraltar during the spawning season. Fromentin and Powers (2005) further suggested that genetic tagging (see, e.g., Palsbøll et al. 1997) might have potential for application to bluefin tuna to directly estimate population parameters, especially F.

The delay between R and SSB under H_K means that for a given fishing mortality, there is a pair of yields and SSB that can affect the consequences of employing biological reference points based on fishing mortality, SSB, and yield (Cook and Heath 2005; Kell et al. 2005*a*, 2005*b*). Delays between F, yield, and SSB (and recruitment) under H_M should also strongly affect estimation of biological reference points. Because of these various lags between SSB and R or F, long-term variations in carrying capacity or migration pattern are likely to influence our capacity to predict future state (e.g., over 15 years) from current perceived status (even if the perception remains unbiased). The evaluation of the performance of VPA stock assessment methods to provide accurate predictions and biological reference points (BRPs) is part of the evaluation of management process, which is the purpose of Kell and Fromentin (2007). More precisely, the performances of BRPs are compared under both hypotheses (H_K and H_M) with respect to their ability to provide accurate estimates of MSY, F_{MSY}, and B_{MSY} and to assess stock status and exploitation level relative to them. In addition, the performance of contrasting management strategies in the face of uncertainty about the true dynamic processes is evaluated.

Acknowledgements

This paper was prepared with funding support provided by the UK Department for Environment, Food and Rural Affairs (DEFRA, under contract M0322) for LTK and by the European Commission Research Directorates through the EU FP5 project FEMS: Framework for Evaluation of Management Strategies (contract Q5RS-2002-01824). The authors thank Dr. A.I.L. Payne for comments and suggestions on early and final drafts.

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Evaluation of the robustness of maximum sustainable yield based management strategies to variations in carrying capacity or migration pattern of Atlantic bluefin tuna (*Thunnus thynnus*)[1]

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Abstract: In this study, we examine the performances of current stock assessment methods with respect to their ability to (*i*) provide estimates of maximum sustainable yield (MSY), F_{MSY}, and B_{MSY} and (*ii*) assess stock status and exploitation level relative to MSY targets. The robustness of the current International Commission for the Conservation of Atlantic Tunas (ICCAT) management strategy is then evaluated with respect to uncertainty about the true population dynamics and contrasted with a simpler management strategy based solely on a size limit. Reference points are more robust to dynamic uncertainty than the estimates of absolute values and trends in F and spawning stock biomass. However, their performances depend on the underlying dynamics (they perform better when fluctuations come from changes in the carrying capacity than migration) and on when they are implemented relative to the intrinsic cycle of the population. Reference points based on F were less biased and more precise than those based on biomass and (or) yield. Although $F_{0.1}$ appeared to be the best proxy for F_{MSY}, it cannot indicate past and current levels of exploitation relative to F_{MSY} when there is uncertainty about the dynamics. Finally, the $F_{0.1}$ management strategy of ICCAT performed only slightly better than a simpler strategy based on size limit and led to lower catch levels.

Résumé : Dans cette étude, nous testons les performances des méthodes d'évaluation des stocks courantes au regard : (*i*) de leur capacité à fournir de bonnes estimations de la production maximale equilibrée (PME), F_{PME} et B_{PME} et (*ii*) d'évaluer l'état du stock et le niveau d'exploitation par rapport à ces points de référence basés sur la PME. Nous évaluons ensuite la robustesse de la stratégie actuelle de gestion de la CICTA (Commission Internationale pour la Conservation des Thonidés de l'Atlantique (basée sur la PME) aux incertitudes sur la dynamique de population et la comparons à une procédure de gestion plus simple basée sur une taille minimale. Les points de référence sont plus robustes aux incertitudes de dynamique que les estimations des valeurs absolues et les tendances de F et de la biomasse reproductrice. Cependant, leurs performances dépendent de la dynamique sous-jacente (les résultats étant meilleurs quand les fluctuations proviennent de changements dans la capacité de charge que lorsqu'ils résultent de changements migratoires) et de la période à laquelle ils sont implémentés par rapport au cycle intrinsèque de la population. Les points de référence basés sur les F sont plus précis et moins biaisés que ceux calculés à partir des biomasses ou captures. Bien que $F_{0.1}$ apparraisse la meilleure approximation de F_{PME}, il reflète cependant mal les niveaux présents et passés de l'exploitation par rapport à F_{PME} quand il existe des incertitudes dans la dynamique. Finalement, la stratégie de gestion de la CICTA ($F_{0.1}$) ne donne des résultats que légèrement meilleurs qu'une plus simple stratégie basée sur une taille limite et conduit systématiquement à des niveaux de captures bien plus bas.

Introduction

Management of tunas must be consistent with the Agreement for the Implementation of the Provisions of the United Nations Convention of the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks (Doulman 1995) and with the precautionary approach (Food and Agricultural Organization of the United Nations (FAO) 1996). Although actual management of Atlantic bluefin tuna (*Thunnus thynnus*) is the responsibility of the International Commission for the Conservation of Atlantic Tunas (ICCAT), whose Convention states that "The Commission may, on the basis of scientific evidence, make recommendations designed to maintain the populations of tuna and tuna-like fishes that may be taken in the Convention area at levels

Received 4 April 2006. Accepted 17 December 2006. Published on the NRC Research Press Web site at cjfas.nrc.ca on 21 June 2007. J19257

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Table 1. List of the various options used to set up the scenarios for the operating model and sampling process.

Operating model and sampling procedures options	
Hypotheses	Recruitment (H_R)
	Migration (H_M)
Amplitude	Equal to that in observed catches
Steepness	0.75
	0.90
Historical Fs	Constant F being equal to 50% of F_{MSY}
	Constant F being equal to F_{MSY}
	Constant F being equal to 150% of F_{MSY}
	Linear increase in effort corresponding to an increase in fishing mortality from 50% of F_{MSY} to 250% of F_{MSY} over a full population cycle, i.e., 110 years.
Phases at starting point	Peak
	Middle of the decreasing slope
	Bottom
	Middle of the increasing slope
Observation error model	Method of Arrizabalaga (2005)
Misreporting	Based on alternative catch used in ICCAT stock assessment (see ICCAT 2003*b*)
Length of runs	A full long-term cycle, i.e., 110 years

which will permit the maximum sustainable catch" (ICCAT 2003*a*). Maximum sustainable catch is generally assumed to be synonymous with maximum sustainable yield (MSY). However, the MSY concept has been criticised by fish biologists for many years, because in many cases, it is not a robust objective in the face of uncertainty (e.g., owing to the natural stochastic variation in biological processes), which can mask the effects of exploitation, so that initial overexploitation is not detectable until it is severe and often irreversible. Rosenberg and Restrepo (1994) showed that stocks managed to provide MSY may not lead to sustainable and (or) optimal management because of uncertainties associated with interpretation of data and the simplifying assumptions made when modelling biological processes. Furthermore, exploitation, even at moderate levels, may induce complex and important modifications in population resistance and resilience through, e.g., changes in habitat, population structure, genetic diversity, or trophic interactions (e.g., Jennings et al. 2002; Birkeland and Dayton 2005). Failure to take such uncertainty into account when using biological reference points may lead to stock collapse, and several fishing-mortality-based reference points have led to unsustainable exploitation (Punt 2000; Dorn 2002).

When long-term fluctuations in catch occur independently from exploitation, Fromentin and Kell (2007) showed that the perception of the stock strongly depends on the underlying mechanism. Where fluctuations were caused by changes in carrying capacity, the stock assessment procedure was able to estimate stock size and fishing mortality rates accurately, but failed if the fluctuations resulted from changes in migration patterns (or availability to fishing). Although the true underlying mechanism is currently unknown, there is knowledge about the biology of bluefin tuna (e.g., they have seasonal spawning and limited spawning grounds) that may make it possible to develop biological monitoring programmes to resolve uncertainty about stock productivity and status (Fromentin and Kell 2007). However, first, it must be determined if current procedures are robust to uncertainty about the dynamics; therefore, in this study we evaluated the performances of stock assessment methods with respect to (*i*) their ability to provide estimates of MSY, F_{MSY}, and B_{MSY} and (*ii*) assessing stock status and exploitation level relative to these MSY targets. We then tested the robustness of the current ICCAT management strategy (i.e., based on MSY) to uncertainty about the true dynamics and historical exploitation levels and contrasted it with a simpler management strategy, with fewer data and less analytical requirements, based on size limits. Finally, we aim to answer the following questions: Can we estimate population status? Can we estimate MSY-based reference points and (or) stock status, relative to these? What are appropriate strategies for achieving management objectives?

Material and methods

The simulation framework used within this study models both the "real" and the "perceived" systems. It therefore implicitly acknowledges the presence of a variety of sources of uncertainty, as categorized by Rosenberg and Restrepo (1994). The "real" stock and fishery dynamics are represented as the operating model, from which simulated data are sampled. These data are used within a management procedure (MP) to (*i*) assess the status of the stock and (*ii*) apply management controls to the fishery and feed back into the "real" system.

The operating model

Assumptions and parameters used to model the population and fleet dynamics in the operating model (OM) were the same as in Fromentin and Kell (2007) and are summarised in Table 1. Again two alternative hypotheses about the OM dynamics were evaluated: the long-term fluctuations observed in trap catches result either from changes in the carrying capacity (or virgin biomass, H_K) or from changes in migratory patterns that affect the proportion of mature bluefin tuna entering the Mediterranean Sea each year to reproduce (H_M). However, here we also considered stochastic variations in recruitment (although no stochasticity was

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included in parameters such as natural mortality, weight-at-age, or selection pattern for clarity and to increase the power to compare performance across scenarios). A Beverton and Holt (1957) stock–recruitment relationship was assumed, with lognormal errors and a coefficient of variation (CV) of 30%, consistent with ICCAT estimates of recruitment variability.

The management procedure

The MP is the specific combination of (*i*) the sampling regime, (*ii*) the stock assessment method, (*iii*) the biological reference points, and (*iv*) the management strategies. Here the MP is based on the ICCAT management regime applied to Atlantic bluefin tuna (ICCAT 2003*b*).

Representing management objectives quantitatively is often one of the most difficult tasks to accomplish when evaluating management strategies as objectives are seldom defined in an operational sense. For example, in the case of ICCAT, the objective is maximum sustainable catch, which although often interpreted as MSY, can be obtained in a variety of ways. In the same way, managers often experience great difficulty in determining how objectives can be expressed quantitatively when managing fleets by effort control or technical measures (Kirkwood and Smith 1996; Sainsbury et al. 2000). There is also often a wide range of possible management objectives largely of a qualitative nature.

Sampling regime

The sampling regime corresponds to the collection of commercial catch data and the derivation of catch numbers-at-age and catch per unit effort (CPUE). These data were generated by the observation error model in which growth, maturity, and natural mortality-at-age were sampled without error from the OM (values were the same as those used in the 2002 stock assessment and did not vary between years; see Fromentin and Kell (2007) for more details). However, catch-at-age was sampled with random error (from a multinomial distribution) based on the study of Arrizabalaga et al. (2005), who used Monte Carlo simulation of monthly catch-at-size data of some fleets to estimate measurement errors in the whole catch-at-age. These data could then be used to estimate the correlations between ages and the mean–variance relationship for each age to derive the covariance matrix for sampled catch-at-age. However, we fixed the CV for all ages at 20% to avoid high variances at some ages (mostly caused by a lack of monitoring).

Assessment method and biological reference points

The stock assessment model used is virtual population analysis (VPA) calibrated using CPUE data, as used to perform bluefin tuna stock assessments by ICCAT (here referred as ADAPT-VPA; Porch 1997; ICCAT 2003*b*). ADAPT-VPA uses total catch-at-age data, conditional on numbers (or fishing mortality) at age of the oldest age in each cohort where the latter is estimated using CPUE from the fishery, to recreate historical numbers and fishing mortality-at-age. It is also assumed that catch and natural mortality are known without error, that there is no immigration or emigration, and that the stock is homogeneous. The VPA was run over 30 years, as this is currently done within ICCAT stock assessments (ICCAT 2003*b*, 2007).

Biological reference points (BRP) chosen for management were all proxies for F_{MSY}, i.e., $F_{0.1}$, F_{max}, $F_{30\%\ SPR}$ and $F_{40\%\ SPR}$, or the corresponding values of MSY and B_{MSY} (calculated from the yield- and spawner-per-recruit curves × the mean recruitment), where $F_{0.1}$ is the value of fishing mortality for which the slope of the yield-per-recruit curve (as a function of F) is 1/10th of the value at the origin, F_{max} is the value of fishing mortality that maximises the yield-per-recruit, and $F_{30\%\ SPR}$ and $F_{40\%\ SPR}$ are the fishing mortalities corresponding to values of fishing mortality where spawner-per-recruit is 30% and 40%, respectively, of virgin spawner-per-recruit (i.e., at zero fishing mortality).

Management strategies

Two contrasting management regimes were considered: (*i*) a harvest control rule (HCR) based on $F_{0.1}$ (mimicking the ICCAT harvest control rule), where the total allowable catch (TAC) is set equivalent to a level of fishing mortality equal to $F_{0.1}$, based on VPA and a short-term forecast; (*ii*) an alternative simple regime based on a change in selection pattern of immature fish (i.e., younger than 5 years) equivalent to a reduction in F of 75% of these ages.

For each experimental scenario, management strategies were run for 15 years into the future (i.e., years 111 to 125), and population parameters and biological reference points were re-estimated using ADAPT-VPA. A 15-year period was chosen because it corresponds to the generation time of Atlantic bluefin tuna (Fromentin and Kell 2007).

ICCAT has previously expressed concern about the quality of the catch and effort data (ICCAT 2003*b*, 2005), and various possible causes for misreporting of catches (including nonreporting by members and nonmember countries) have been postulated. One of the main reasons for misreporting appears to be related to the implementation of quotas for East Atlantic and Mediterranean bluefin tuna in 1996 and 1998 (Fromentin and Powers 2005). It was subsequently believed that this resulted in over-reporting before the period 1996–1998 and under-reporting since. Although little quantitative information is available to characterize misreporting precisely, ICCAT proposed an alternative catch scenario, based on 15% over-reporting for the period 1993–1997 and 15% under-reporting from 1998 onwards, in order to conduct sensitivity trials during the last stock assessment (ICCAT 2003*b*). We therefore added an implementation error model to reflect the fact that current harvest control rules may be poorly endorsed using the same scenario as that applied in the 2002 stock assessment.

All experimental scenarios (including the four historical fishing mortalities, the four starting points, and the two steepness values and the possibility (or not) of misreporting) generate 64 simulations for each hypothesis (H_R and H_M; see Table 1). For each scenario, 1000 Monte Carlo simulations were run, with random variables as stated above. Stochastic runs including recruitment and observation error were performed for 1000 simulations.

Results

All the scenarios (with their Monte Carlo simulations) are summarised and compared by inspection of box-and-whisker plots (Figs. 1 to 5), where the performance of the MP is evaluated by dividing the examined indicator estimated from the

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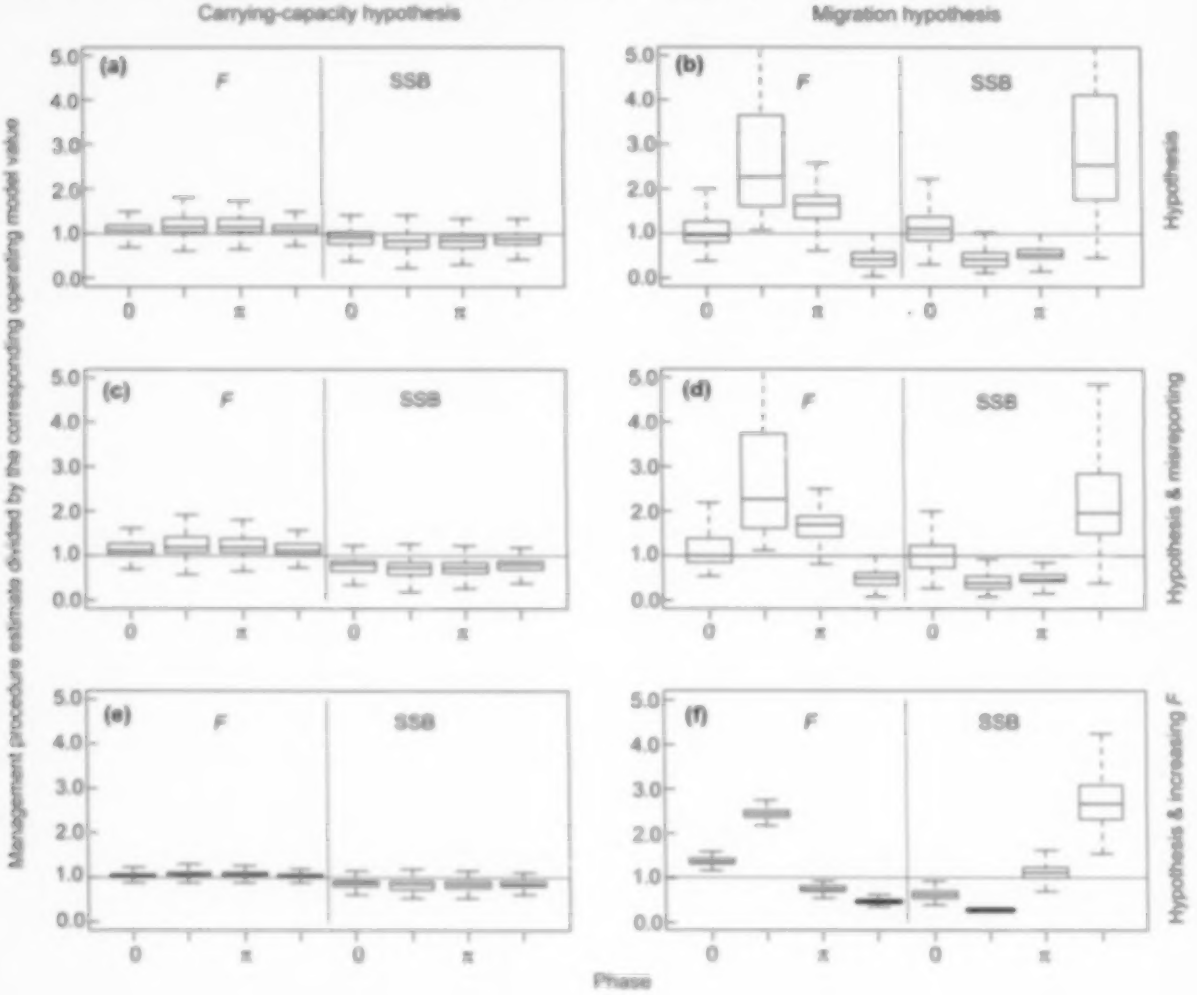
Fig. 1. Performance in assessing stock status relative to F and spawning stock biomass (SSB) by hypothesis (carrying capacity and migration) and phase under misreporting and increasing F scenarios (simulations include stochastic recruitment in the operating model and random errors in the catch-at-age in the sampling procedure). Scenarios are compared by inspection of box-and-whisker plots where the performance of the management procedure (MP) is evaluated by dividing the examined indicator estimated from the MP by the corresponding true value of the operating model (OM) so that unbiased and precise MP estimates will lead to values close to 1.0 with low variance. Boxes show the interquartile range and median, whiskers represent 1.5 times the interquartile range. (*a*) All scenarios with constant historical Fs under the carrying-capacity hypothesis (H_K); (*b*) all scenarios with constant historical Fs under the migration hypothesis (H_M); (*c*) same as (*a*) with misreporting; (*d*) same as (*b*) with misreporting; (*e*) all scenarios with increasing historical Fs under the H_K; (*f*) all scenarios with increasing historical Fs under the H_M.



MP by the corresponding true value of the OM so that unbiased and precise MP estimates will lead to values close to 1.0 with low variance. Boxes show the interquartile range and medians, whiskers indicate 1.5 times the interquartile range.

Ability to detect population status

The ability of the MP to estimate F and SSB is evaluated in Fig. 1, but in comparison with Fromentin and Kell (2007), these simulations also include stochastic recruitment in the operating model and random errors in the catch-at-age in the sampling procedure (see above). As expected from Fromentin and Kell (2006), the main difference results from the underlying hypothesis (i.e., carrying capacity, H_K, or migration, H_M). Whatever the scenario (i.e., constant F, misreporting, or increasing F), the box plots under H_M display both strong bias and large variability, reflecting the poor performance of VPA under this hypothesis. Phases in the cycle of the biological process hypothesised (or initial conditions of the VPA) are also clearly important, because for some phases ($\pi/2$ and $3\pi/2$), the bias in SSB can be greater than 300%, whereas for another starting point (0), the performance of the VPA appears to be better (Figs. 1*b*, 1*d*, 1*f*). In contrast, the MP under H_K exhibits low bias and more precise F and SSB trends in all cases. The effect of

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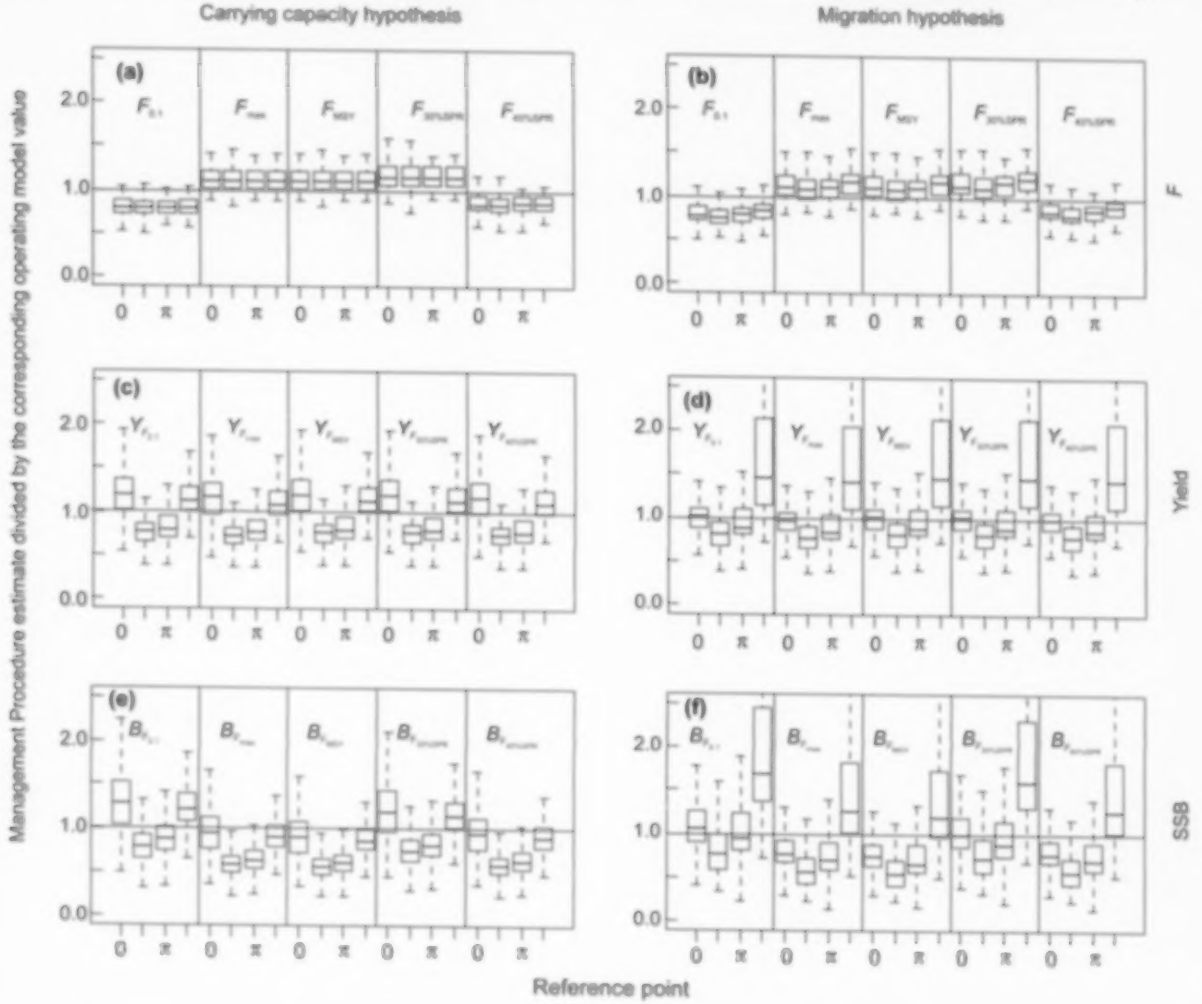
Fig. 2. A comparison of maximum sustainable yield (MSY) based biological reference points (BRP) estimated by the management procedure and divided by the corresponding true (i.e., operating model, OM) values of F_{MSY}, MSY, and B_{MSY}. (*a*) BRP based on F under the carrying-capacity hypothesis (H_K); (*b*) BRP based on F under the migration hypothesis (H_M); (*c*) BRP based on yield under H_K; (*d*) BRP based on yield under H_M; (*e*) BRP based on spawning stock biomass (SSB) under H_K; (*f*) BRP based on SSB under H_M.



misreporting appears to be relatively minor compared with the hypothesis about the dynamics and the effect of the starting point (although the variability strongly increases under H_M; Figs. 1*c*, 1*d*). Increasing historical Fs (Figs. 1*e*, 1*f*; as steepness (results not shown)) have little effect. These results thus confirm that the MP consistently fails to estimate accurately trends in F and SSB under H_M (and can further give an optimistic perception of the stock in some cases), but it performs well in most cases under H_K, even when misreporting is assumed.

Performance of reference points

The performance of the MP in providing proxies of MSY, F_{MSY} and B_{MSY} is evaluated (Fig. 2). For each hypothesis and each phase, a range of proxies for F_{MSY} was calculated within the MP (i.e., $F_{0.1}$, F_{max}, $F_{30\%\ SPR}$, $F_{40\%\ SPR}$), along with the corresponding proxies for B_{MSY} and MSY (derived from yield- and spawner-per-recruit assuming that recruitment was equal to the mean of the last 5 years). Here again, ratios close to 1 indicate good performance of the MP. In contrast to Fig. 1, the differences between hypotheses (H_M and H_K) are not so critical, especially for BRPs based on F (Figs. 2*a*, 2*b*). In other words, the performances of the BRPs appear to be more robust to uncertainty in the dynamics than are the stock assessment estimates (Figs. 1, 2). This is because BRP are based on equilibrium calculations and selectivity patterns, which are biased by factors other than the underlying dynamics. The biggest difference between scenarios is for initial conditions (i.e., phases between exploitation and natural long-term cycle), i.e., is availability or carrying capacity currently increasing (decreasing) or at a peak (nadir). However, the variability remains much higher under H_M than under H_K, especially for yield- and SSB-based BRP (Figs. 2*d*, 2*f*). In general, $F_{0.1}$ (and secondarily

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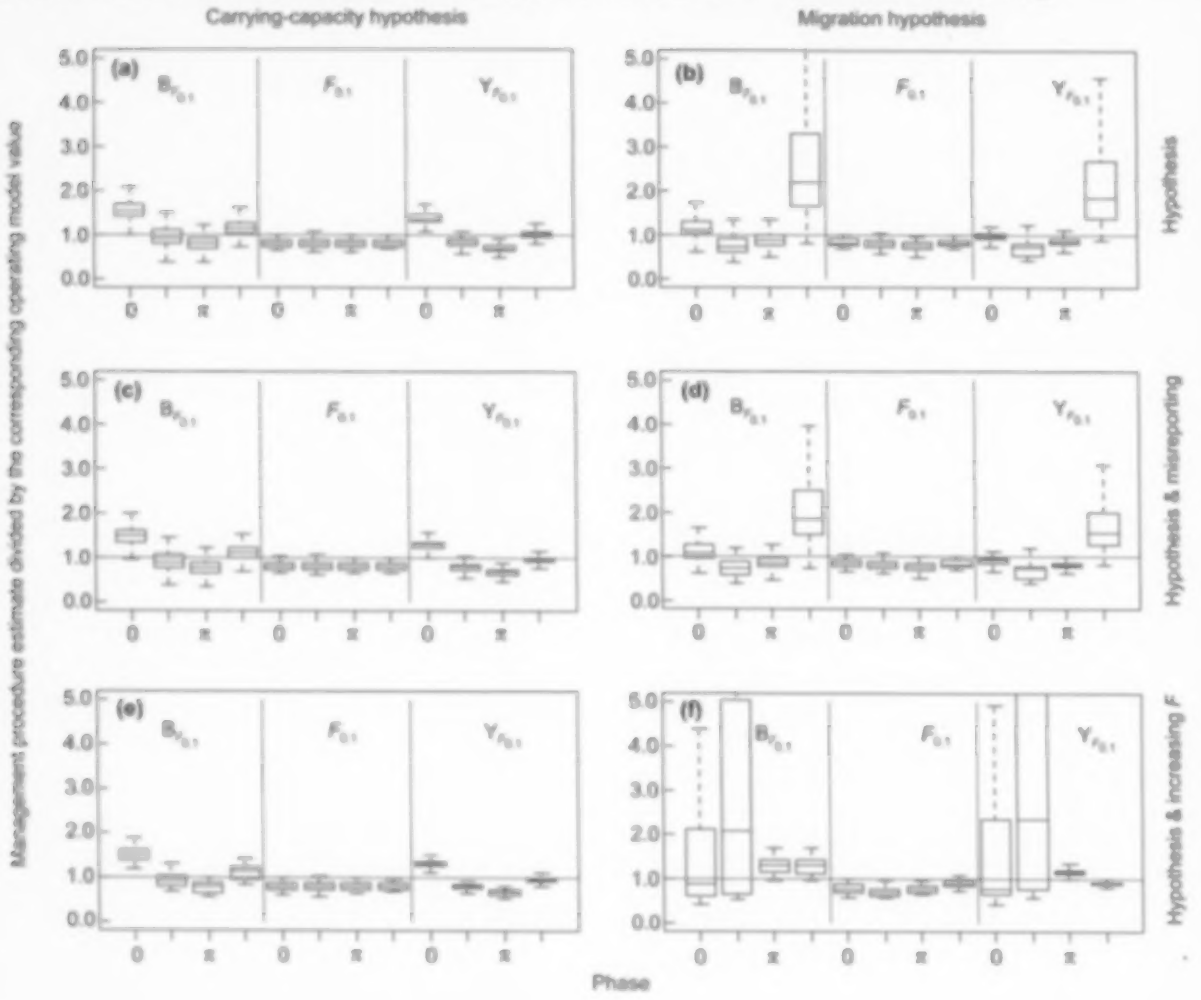
Fig. 3. A comparison of $F_{0.1}$-based reference points (estimated by the management procedure) divided by the corresponding true (i.e., operating model, OM) F_{MSY}. (*a*) All scenarios with constant historical *F*s under the carrying-capacity hypothesis (H_K); (*b*) all scenarios with constant historical *F*s under the migration hypothesis (H_M); (*c*) same as (*a*) with misreporting; (*d*) same as (*b*) with misreporting; (*e*) all scenarios with increasing historical *F*s under the H_K; (*f*) all scenarios with increasing historical *F*s under the H_M.



$F_{SPR\ SPR}$) gives better and more consistent results than the other BRPs ($F_{0.1}$ values are indeed always around 1 and display little variance among scenarios; Fig. 2). $F_{0.1}$ therefore appeared to be the best proxy for F_{MSY}, so subsequent analyses are only presented for $F_{0.1}$.

The $F_{0.1}$-based reference points from the MP (i.e., $B_{F_{0.1}}$, $F_{0.1}$, $Y_{F_{0.1}}$) divided by the corresponding MSY-based quantity from the OM (i.e., B_{MSY}, F_{MSY}, MSY) are presented (Fig. 3). The performances of $F_{0.1}$-based reference points in providing a good proxy for F_{MSY} is generally better under H_K than under H_M, especially for increasing *F* scenarios (Figs. 3*e*, 3*f*). For some phases, biomass- and yield-based reference points ($B_{F_{0.1}}$ and $Y_{F_{0.1}}$) are strongly biased (up to 200%) and can further display large variability (especially for increasing *F* under H_K; Fig. 3*f*). By contrast, $F_{0.1}$ reference points are more consistent among starting points and hypotheses. They are always precise (i.e., they display little variability) and are only slightly biased (but consistently underestimated). Misreporting has little effect on the performances of all $F_{0.1}$-based reference points. In summary, therefore, $F_{0.1}$ appears to be more accurate (i.e., less biased and more precise) than reference points based on biomass or yield ($B_{F_{0.1}}$ and $Y_{F_{0.1}}$).

Even if estimates of *F* and SSB (Fig. 1), reference points (Fig. 2), and $F_{0.1}$ relative to F_{MSY} (Fig. 3) are biased, reference points may still perform well in indicating whether the stock biomass is below B_{MSY} or whether *F* is above F_{MSY}. Therefore, we evaluated the performance of relative indicators defined by the ratio of *F*, SSB, and yield to their corresponding $F_{0.1}$-based reference points (again by dividing these ratios to corresponding ratios from the OM), e.g., $\frac{\bar{F}:F_{0.1}}{F:F_{MSY}}$ (where $\bar{F}$ is the mean value of *F* of the MP over the

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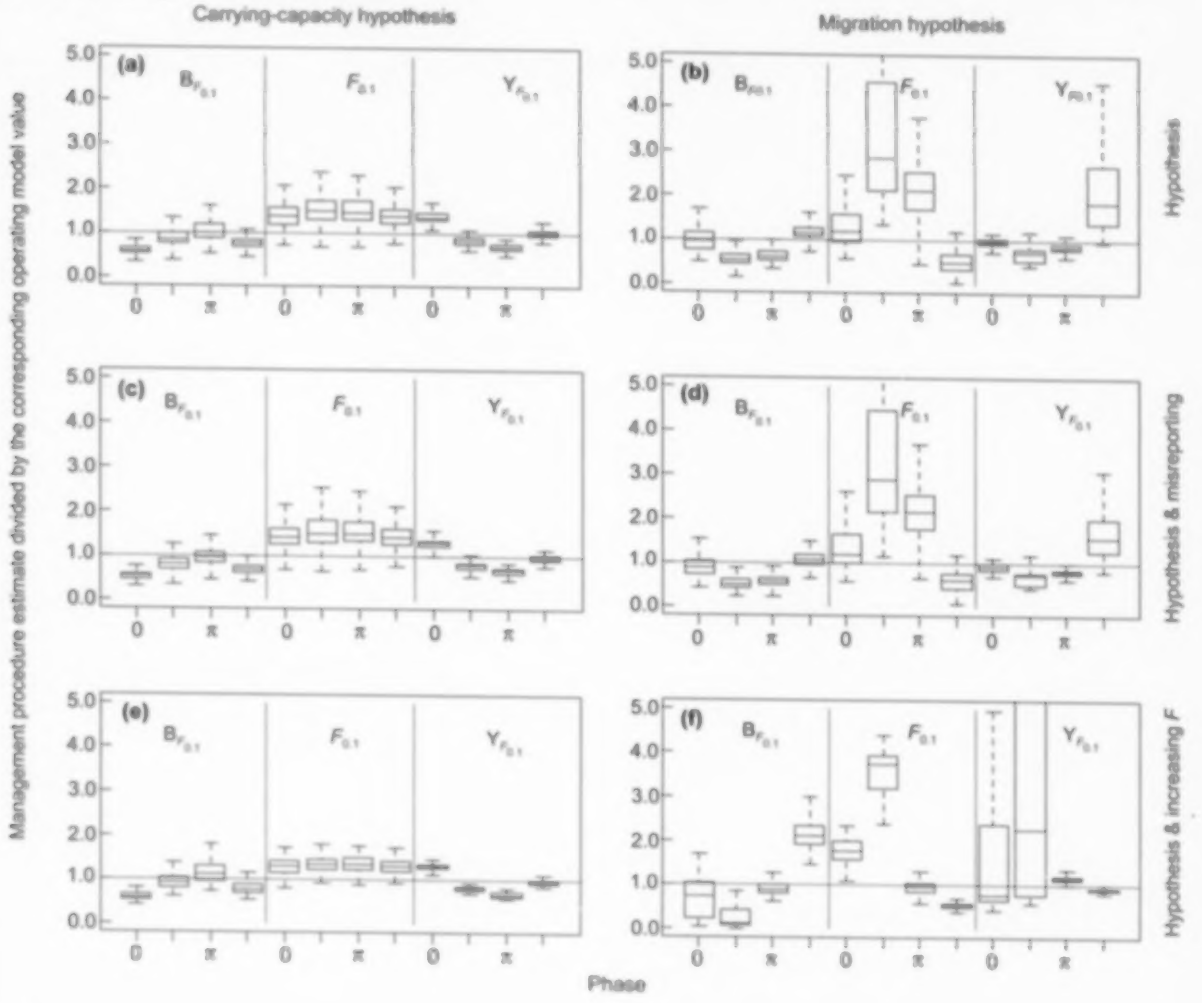
Fig. 4. A comparison of the ratios of F, spawning stock biomass (SSB), and maximum sustainable yield to their corresponding $F_{0.1}$-based reference points divided by the corresponding ratios from the operating model) e.g., $\frac{\bar{F}:F_{0.1}}{F:F_{MSY}}$ ($\bar{F}$ being the mean value of F of the management procedure (MP) over the past 5 years). (*a*) All scenarios with constant historical Fs under the carrying-capacity hypothesis (H_K); (*b*) all scenarios with constant historical Fs under the migration hypothesis (H_M); (*c*) same as (*a*) with misreporting; (*d*) same as (*b*) with misreporting; (*e*) all scenarios with increasing historical Fs under the H_K; (*f*) all scenarios with increasing historical Fs under the H_M.



past 3 years, as performed by ICCAT, as recent VPA estimates are the most uncertain). In contrast to previous results (i.e., estimates of $F_{0.1}$ relative to F_{MSY}), F-based quantities exhibit the greatest biases and, most often, the largest variations (Figs. 4*b*, 4*d*, 4*f*). Both hypothesis and starting point are important in determining the accuracy of these estimates, which are again more biased and much less precise under H_M than under H_K, because VPA performs poorly under H_M (see above). Here again, misreporting has little effect on the performance of F-based quantities, but increasing historical Fs have. In summary, the F-based quantities (i.e., F relative to $F_{0.1}$) lead to unreliable estimates (especially under H_M) and are more biased and more variable than $F_{0.1}$-based reference points. Consequently, it appears risky to indicate past and current levels of exploitation relative to F_{MSY} when there is uncertainty about the actual dynamics.

Evaluation of management procedures

The evaluation of reference points is best performed as part of a management procedure that includes the harvest control rule and stock assessment method (Kell et al. 2006). Therefore, the performances of an $F_{0.1}$-based MP was evaluated and compared with the status quo (i.e., current effort levels) and an alternative in which selection pattern (rather than F) was the management variable in Fig. 5. The $F_{0.1}$-based MP is an attempt to implement ICCAT management

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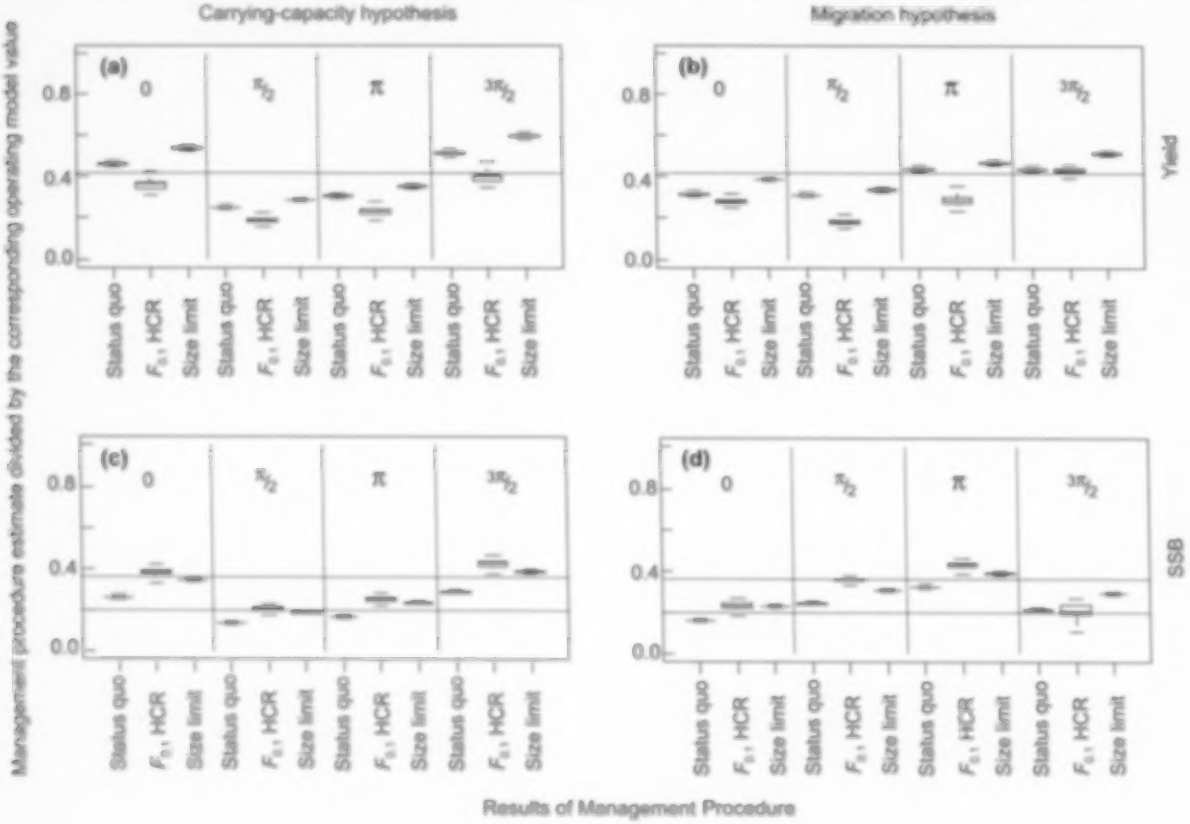
Fig. 5. Comparison of a management procedure (MP) based on a harvest control rule (HCR) based on $F_{0.1}$ ($F_{0.1}$ HCR) with a MP based on size limit regulation (size limit), when considering constant historical Fs equivalent to 150% F_{MSY}. Status quo assumes no regulation. Yield or spawning stock biomass (SSB) of each MP is given relative to the maximum possible yield and to virgin biomass, respectively. The maximum yield is found by harvesting all fish when production attributable to growth becomes less than that lost to natural mortality; for Atlantic bluefin this is at age 13 (under H_M, MSY is 17 500, but the maximum yield is 42 500). (*a*) Comparison of MPs in terms of yield under the carrying-capacity hypothesis (H_K); (*b*) same as (*a*) under the migration hypothesis (H_M); (*c*) comparison of MP in terms of SSB under the carrying-capacity hypothesis (H_K); (*d*) same as (*c*) under the migration hypothesis (H_M).



objectives in a harvest control rule intended to achieve MSY. In contrast, the alternative MP solely relies on size limit regulation and does not modify fishing effort (the size limit set at age-at-maturity, i.e., 5 years, with a 25% of tolerance for younger ages to take into account fisheries targeting juveniles).

Performances of both MPs were based on summary statistics from the OM after 15 years of implementation (one generation time) and were evaluated by comparison with the status quo (i.e., no regulation). The results are depicted by phases when considering constant historical Fs equivalent to 150% F_{MSY}, which is a scenario closer to the current fishing pressure than the others, i.e., 50% and 100% F_{MSY} (Fromentin and Powers 2005). As MSY depends on the selectivity pattern of the fleets (e.g., Powers 2005), yield is expressed relative to maximum possible yield and SSB relatively to virgin biomass. In addition, MSY, B_{MSY} (calculated for the current selectivity pattern), and the biomass level corresponding to 75% of the "virgin recruitment" (i.e., biomass limit for recruitment–overfishing when the steepness of the stock–recruitment relationship equals 0.75, denoted $B_{75\%\,R}$) are shown as horizontal lines for comparison.

Relative yields under both management strategies vary between 20% and 60% of the maximum yield. Differences appear to be due mostly to management strategy and starting point and less to the underlying hypothesis (H_M or H_K). Although higher yields are seen under H_K, the range of yields remains indeed similar under both hypotheses. Regarding the MP, expected yields are always highest under the size limit strategy (up to 60% of maximum yield), second highest under status quo, and lowest under the $F_{0.1}$ strategy (where they do not exceed 40% of the maximum yield; Figs. 5*a*, 5*b*). However, the performance of a given management strategy also depends on when it is implemented relative to the intrinsic cycle of the population. The expected SSBs are in general similar to or slightly higher under the $F_{0.1}$ than under the size limit strategy (Figs. 5*c*, 5*d*). Depending on starting points, SSBs are at 40% (about B_{MSY}) or 20% (about $B_{75\%\,R}$) of virgin biomass. Under the size limit strategy, SSB is always greater than the status quo, and in all the cases but

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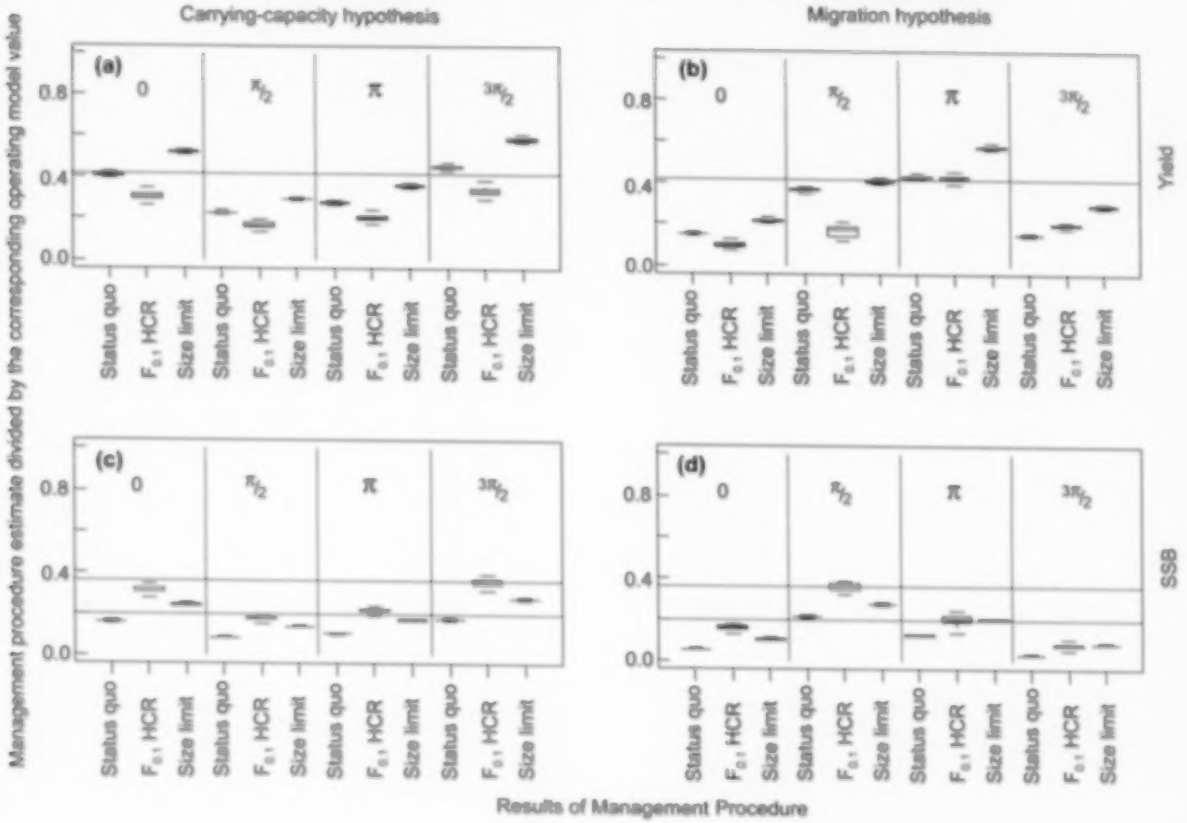
Fig. 6. Comparison of a management procedure (MP) based on a harvest control rule (HCR) based on $F_{0.1}$ ($F_{0.1}$ HCR) with a MP based on size limit regulation (size limit), when considering increasing historical *F*s. Status quo assumes no regulation. Yield or spawning stock biomass (SSB) of each MP is given relative to the maximum possible yield and to virgin biomass, respectively. The maximum yield is found by harvesting all fish when production attributable to growth becomes less than that lost to natural mortality; for Atlantic bluefin this is at age 13 (under H_M, MSY is 17 500, but the maximum yield is 42 500). (*a*) Comparison of MPs in terms of yield under the carrying-capacity hypothesis (H_K); (*b*) same as (*a*) under the migration hypothesis (H_M); (*c*) comparison of MP in terms of SSB under the carrying-capacity hypothesis (H_K); (*d*) same as (*c*) under the migration hypothesis (H_M).



one, SSB remains greater than 20% virgin (a potential recovery level). The status quo generally leads to the lowest SSBs, which are sometimes under the 20% virgin limit.

Evaluation of the effect of increasing historical *F*s instead of constant *F*s is performed (Fig. 6), and it can be seen that yield patterns are comparable under H_K, but not under H_M, for which yields are clearly lower (and often below 20% maximum yield; Figs. 6*a*, 6*b*). Again yields were higher under the size limit than under the $F_{0.1}$ strategy, but SSBs were generally lower (below 20% virgin in many cases; Figs. 6*c*, 6*d*). Here again the performance of a given MP (for both yield and SSB) depends on when it is implemented relative to the intrinsic cycle of the population. Although performance was poor for both hypotheses, both MPs performed better than the control. Notwithstanding, problems were more acute under H_M because of the opposition of phase between *F* and SSB (Fromentin and Kell 2007), which means that increasing effort can reinforce depletion for some starting points.

A size limit strategy generates greater yields than the more sophisticated $F_{0.1}$ but lower SSBs in some cases. Further, more important than the underlying process (H_M or H_K) was the current phase of the cycle, because this strongly affected the performances of both management strategies.

Discussion

Fromentin and Kell (2007) showed that the ability to estimate stock size and fishing mortality accurately depends on the underlying processes that may cause long-term variation in the catches. The same conclusion is reached in this study, in which stochasticity in recruitment and sampling procedure, as well as implementation error (i.e., misreporting), were also incorporated. Where fluctuations are caused by changes in carrying capacity, the stock assessment procedure is able to estimate stock size and fishing mortality rate accurately, but fails in most cases if the fluctuations result from changes in migration pattern (i.e., availability to fishing). In other words, uncertainty about the true dynamics was more critical to the process than the assumed uncertainty attribut-

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able to misreporting and stochasticity in some biological processes.

The study demonstrated the following for both hypotheses (H_M and H_K): (*i*) $F_{0.1}$ was the best proxy for F_{MSY} (performing better than F_{max} and $F_{30\%\ SPR}$); (*ii*) reference points based on F (e.g., $F_{0.1}$) were less biased and more precise than those based on yield and (or) SSB, e.g., $Y_{F_{0.1}}$ or $B_{F_{0.1}}$; and (*iii*) F-based reference points were more robust to uncertainty about the true dynamics than absolute estimates in fishing mortality and SSB, but (*iv*) their ability to predict exploitation level relative to F_{MSY} was poor (and less than those based on yield and (or) SSB). Therefore, reference points such as $F_{0.1}$ appear to be more robust to dynamic uncertainty than absolute estimates of F and SSB and perform, as a whole, satisfactorily. Unfortunately, however, $F_{0.1}$ cannot indicate past and current levels of exploitation relative to F_{MSY} when there is uncertainty about the dynamics. Therefore, although reference points such as $F_{0.1}$ may be good proxies for F_{MSY}, the MSY concept may be difficult to make operational when trends in yield can occur, either through variations in carrying capacity (H_K), migration (H_M), or effort.

Traditionally, MSY-based strategies are conditional upon a mean selection pattern in the fishery, which in practice assumes fixed effort allocation between fleets. However, the maximum catch is actually found when all individuals above a certain age are harvested (Beddington and May 1977), i.e., when losses attributable to natural mortality become greater than the gains through growth. As Powers (2005) pointed out, the determination of reference points (such as MSY) depends on the selectivity of the various fleets, the relative mix of fleets that management desires, and any bycatch in nontarget fisheries. This could be achieved either by changing the relative fleet composition (i.e., reducing the effort of fleets targeting juvenile fish) or by forcing existing fleets to be more selective (e.g., imposing a size limit on the catch). The actual choice depends as much on socio-economic and operational factors as on biological considerations. Therefore, economic and biological objectives need to be stated explicitly, so that trade-offs between risk to a stock, yield levels, and employment opportunities can be fully evaluated across fleets and national sectors.

An alternative to an $F_{0.1}$ strategy could be simply setting a size limit with or without constraints on effort. This would also require less knowledge about stock dynamics and might provide an alternative that is more robust to uncertainty about biological processes. An additional benefit would be that the logic of allowing more fish to spawn at least once would be more transparent than a management strategy based on VPA, F_{MSY} (or $F_{0.1}$), and catch quotas.

An evaluation of alternative management strategies was performed through simulation in order to take the various sources of uncertainty into account, including lack of knowledge about dynamic processes, consistent with the principles of the precautionary approach (FAO 1996). When the $F_{0.1}$-based MP and an alternative based on a size limit were evaluated with respect to uncertainty about the true dynamics, the performances of both management strategies were quite similar but strongly dependent on the phases, i.e., the period over which they are implemented relative to the intrinsic cycle of the population. However, as stock size does not fluctuate synchronously with the catch under H_M and as we cannot determine the real underlying process without fishery-independent data or scientific study (see Fromentin and Kell 2007), it will be difficult to determine what the true dynamics are or even what phase the cycle is in. It will therefore be difficult to distinguish between natural and anthropogenic changes, to detect changes in productivity, and to revise reference points without fishery-independent data and targeted scientific studies on the biology and ecology of the population. Note also that Fromentin and Kell (2007) showed that there may be no simple stock–recruitment relationship if SSB is lagged with recruitment.

An $F_{0.1}$ MP based on ADAPT-VPA stock size estimates only performed slightly better than a strategy based on a simple size limit. Further, the former led to much lower catch levels than the latter. Note, however, that yield and SSB are not strictly comparable, because reference points under the two management scenarios would be different. Although under the $F_{0.1}$ strategy B_{MSY} is not an appropriate target, a biomass limit may be more appropriate for the size limit strategy, because it would be more important to ensure that recruitment is not impaired rather than that the stock is at B_{MSY}. For example, an appropriate biomass limit in the case of a stock–recruitment relationship with a steepness value of 0.75 might be 20% of virgin biomass, because at this level, recruitment need only be 75% of the unexploited level. However, such a limit would have to be decided upon taking uncertainty and management objectives into account.

Finally, the performances and robustness of distinct management strategies depend on (*i*) biological processes (i.e., the underlying dynamics), (*ii*) phases (when they are implemented relative to the stock size cycle), and also (*iii*) concrete objectives, such as fleet composition, gear selectivity, and economic constraints. For example, the two management strategies have different implications for choice of reference points; the $F_{0.1}$ strategy is based on a target fishing mortality and hence effort, whereas the size limit strategy has an implicit biomass limit (i.e., the minimum biomass of immature fish). The two strategies also imply different management objectives. For example, a size limit strategy will reduce effort or yield for certain fleets more than others, whereas an $F_{0.1}$ strategy implies an equal cut in effort by all fleets. The choice of a strategy cannot therefore be decided on a purely scientific basis, but rather through its performances relative to the main management objectives, fisheries constraints, and biological and ecological processes postulated (Powers and Porch 2004; Kell et al. 2005). Such investigations are best conducted through the type of simulations of management strategies performed in this study.

Options are to develop management strategies that are robust to uncertainty about the dynamics (e.g., a size-selectivity management strategy), to reduce uncertainty by improving biological knowledge (e.g., use of new techniques to monitor spawning ground or migration routes such as listening stations along the Gibraltar Strait or the large-scale tagging of juvenile fish with electronic chips), or to develop more elaborate population dynamics models such as a VPA that includes spatial stratification and the statistical estimate of migration coefficient between the Atlantic and Mediterranean Sea. However, difficulties in

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implementation of management regulations and therefore uncertainty about actual catches may make it difficult to use such an assessment method. Development of such methods should be simulation tested to evaluate their robustness to model assumptions and uncertainty about the data.

An incentive to resolve uncertainty could be provided by a strict implementation of the precautionary approach, i.e., by ensuring that there is a positive relationship between information and utilisation (Cooke 1999), so that the less known, the lower the level of exploitation. This means that there would be an incentive to resolve key uncertainties about the population dynamics by conducting appropriate scientific investigations or to develop robust alternatives. Only in this way can strategies be developed that are robust to uncertainty about our knowledge of stock dynamics and the ability to control fisheries, including noncompliance with regulations.

Acknowledgements

This paper was prepared with funding support provided by the UK Department for Environment, Food and Rural Affairs (DEFRA, under contract M0322) for LTK and by the European Commission Research Directorates through the EU FP5 project FEMS: Framework for Evaluation of Management Strategies (contract Q5RS-2002-01824). The authors thank Dr. A.I.L. Payne for comments and suggestions on earlier and final drafts.

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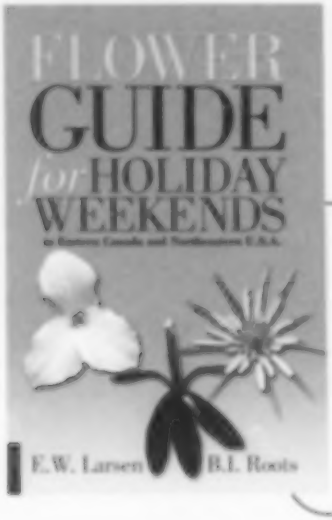

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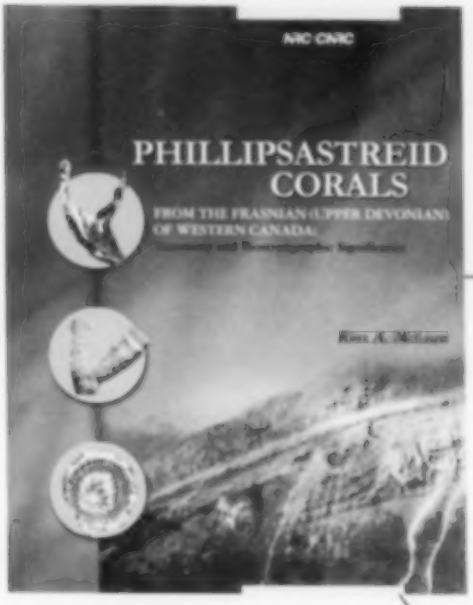

Phillipsastreid Corals

from the Frasnian (Upper Devonian) of Western Canada: Taxonomy and Biostratigraphic Significance

By / Par
Rose A. McLean

109 Pages 2005
Softcover / Édition brochée

ISBN 0-660-19364-7; NRC 46847
ISBN 0-660-19364-7; CNRC 46847

$49.95 CAN; Other countries: $49.95 US
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Rugose corals of the Family Phillipsastreidae are abundant, diverse, and geographically widespread in the Frasnian (lower Upper Devonian) of western Canada. Species of the solitary genus Macgeea are described. Thamnophyllum and Peneckiella are branching forms. Biostratigraphic distribution of these species is reviewed, together with that of previously described Canadian massive phillipsastreid species belonging to the genera Phillipsastrea, Chuanbeiphyllum, Pachyphyllum, Smithicyathus, and Frechastraea. The coral biostratigraphy is expressed in terms of the Montagne Noire conodont zonation and modified western Canada rugose coral faunal assemblages.

Les coraux rugueux de la famille des Phillipsastreidae sont abondants, diversifiés et répandus sur le plan géographique dans le Frasnien (étage de base du Dévonien supérieur) de l'Ouest du Canada. L'ouvrage expose les espèces appartenant au genre solitaire Macgeea. Les genres Thamnophyllum et Peneckiella sont des formes branchues. La répartition biostratigraphique de ces espèces est examinée, ainsi que celle d'espèces massives de Phillipsastreidae canadiennes déjà décrites appartenant aux genres Phillipsastrea, Chuanbeiphyllum, Pachyphyllum, Smithicyathus et Frechastraea. La biostratigraphie des coraux est présentée suivant la zonation des conodontes de la Montagne Noire etles assemblages fauniques modifiés de coraux rugueux de l'Ouest du Canada.

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Port payé à Ottawa
Poste-publication
Enregistrement n° 40062591

USPS periodical postage paid at Plattsburgh, NY 12901, USA

Canadian Journal of Fisheries and Aquatic Sciences

Volume 64, Number 5, May 2007

Journal canadien des sciences halieutiques et aquatiques

Volume 64, numéro 5, mai 2007

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0706-652X(200705)64:5;1-W